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NEW OSTEOGLOSSOMORPHS (TELEOSTEI) FROM THE UPPER CRETACEOUS AND LOWER TERTIARY OF NORTH AMERICA AND THEIR PHYLOGENETIC SIGNIFICANCE

BY

LI GUO-QING ©

A THESIS SUBMITTED TO THE
FACULTY OF GRADUATE STUDIES AND RESEARCH IN
PARTIAL FULFILMENT OF THE REQUIREMENTS FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

Department of Biological Sciences
Edmonton, Alberta, Canada

Fall 1994

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Political Science	
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Public Administration	0617
Recreation	0814
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Sociology	
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General	0473
Agronomy	0285
Animal Culture and Nutrition	0475
Animal Pathology	0476
Food Science and Technology	0359
Forestry and Wildlife	0478
Plant Culture	0479
Plant Pathology	0480
Plant Physiology	0817
Range Management	0777
Wood Technology	0746
Biology	
General	0306
Anatomy	0287
Biostatistics	0308
Botany	0309
Cell	0379
Ecology	0329
Entomology	0353
Genetics	0369
Limnology	0793
Microbiology	0410
Molecular	0307
Neuroscience	0317
Oceanography	0416
Physiology	0433
Radiation	0821
Veterinary Science	0778
Zoology	0472
Biophysics	
General	0786
Medical	0760

EARTH SCIENCES

Biogeochemistry	0425
Geochemistry	0996
Geodesy	0370
Geology	0372
Geophysics	0373
Hydrology	0388
Mineralogy	0411
Paleobotany	0345
Paleoecology	0426
Paleontology	0418
Paleozoology	0985
Palynology	0427
Physical Geography	0368
Physical Oceanography	0415

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Health Sciences	
General	0566
Audiology	0300
Chemotherapy	0992
Dentistry	0567
Education	0350
Hospital Management	0769
Human Development	0758
Immunology	0982
Medicine and Surgery	0564
Mental Health	0347
Nursing	0569
Nutrition	0570
Obstetrics and Gynecology	0380
Occupational Health and Therapy	0354
Ophthalmology	0381
Pathology	0571
Pharmacology	0419
Pharmacy	0572
Physical Therapy	0382
Public Health	0573
Radiology	0574
Recreation	0575
Speech Pathology	0460
Toxicology	0383
Home Economics	0386

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Pharmaceutical	0491
Physical	0494
Polymer	0495
Radiation	0754
Mathematics	0405
Physics	
General	0605
Acoustics	0986
Astronomy and Astrophysics	0606
Atmospheric Science	0608
Atomic	0748
Electronics and Electricity	0607
Elementary Particles and High Energy	0798
Fluid and Plasma	0759
Molecular	0609
Nuclear	0610
Optics	0752
Radiation	0756
Solid State	0611
Statistics	0463

Applied Sciences

Applied Mechanics	0346
Computer Science	0984
Engineering	
General	0537
Aerospace	0538
Agricultural	0539
Automotive	0540
Biomedical	0541
Chemical	0542
Civil	0543
Electronics and Electrical	0544
Heat and Thermodynamics	0348
Hydraulic	0545
Industrial	0546
Marine	0547
Materials Science	0794
Mechanical	0548
Metallurgy	0743
Mining	0551
Nuclear	0552
Packaging	0549
Petroleum	0765
Sanitary and Municipal	0554
System Science	0790
Geotechnology	0428
Operations Research	0796
Plastics Technology	0795
Textile Technology	0994

PSYCHOLOGY

General	0621
Behavioral	0384
Clinical	0622
Developmental	0620
Experimental	0623
Industrial	0624
Personality	0625
Physiological	0989
Psychobiology	0349
Psychometrics	0632
Social	0451

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled NEW OSTEOGLOSSOMORPHS (TELEOSTEI) FROM THE UPPER CRETACEOUS AND LOWER TERTIARY OF NORTH AMERICA AND THEIR PHYLOGENETIC SIGNIFICANCE submitted by LI GUO-QING in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY.

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Dedicated with deepest reverence to the memory of
my mother, Dong You-zhen (1919-1979),
and
my father, Li Xi-sheng (1914-1968),
whose heart's blood and energies were all shed and exhausted
for the education of their children!

ABSTRACT

Two new genera (Osteoglossidae: †*Cretophareodus* gen. nov. and †*Joffrichthys* gen. nov.) and one new species (Hiodontidae: †*Hiodon consteniorum* sp. nov.) are added to the fossil record of Osteoglossomorpha.

†*Cretophareodus* gen. nov. is characterized by its mouth corner being at the level of the posterior margin of the orbit, a six-rayed pectoral fin, a dorsal fin larger than the anal fin and supported by 21 pterygiophores, an opercle with a depth to width ratio about 1.72, and subcycloid scales with fine growth lines interrupted by basal and apical radii. It appears to have shared a recent common ancestor with †*Phareodus*.

†*Joffrichthys* gen. nov. differs from Recent osteoglossids in having an articulation facet for the quadrate on both the retroarticular and anguloarticular, its mouth corner at the level of the vertical midline of orbit, "H"-shaped caudal vertebrae, small pectoral fins, equal-sized dorsal and anal fins, and cycloid scales with central foci and fine circuli interrupted by basal radii. It is likely the sister group of the clade consisting of †*Sinoglossus*, *Heterotis,* and *Arapaima.*

†*Hiodon consteniorum* sp. nov. bridges the gap between †*Eohiodon* and *Hiodon* in both morphology and phylogeny. It contributes to knowledge of the evolution of the hiodontid postcranial skeleton. †*Eohiodon falcatus* is synonymized with †*E. woodruffi.*

The validity of three †*Phareodus* species is clarified. †*P. queenslandicus* is likely the sister-species of †*P. encaustus.* The supposed relationship between hiodontids and notopterids (as well as lycopterids) is not valid. †*Singida* and *Pantodon* are linked with Osteoglossinae. †*Ostariostoma* appears most closely related to Momyroidea.

Osteoglossomorpha are a monophyletic group and the sisterclade of Clupeomorpha plus Euteleostei. The oldest fossils known in East Asia, North America, Africa, South America, and possibly also Australia suggest that the hypothetical earliest ancestral osteoglossomorphs could have well existed much earlier and had a much more widespread distribution than any of those Late Jurassic or Early Cretaceous genera. Consequently, Osteoglossomorpha might have accomplished their early evolution in Pangaea by the time of the Late Jurassic, before the final splitting of that supercontinent.

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nov. for this study, and for permission to examine the ROM collection; and to Dr. R. E. Molnar at Queensland Museum, Queensland, Australia, for the loan of casts of †*Phareodus queenslandicus* for comparative purposes.

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CONTENTS

Chapter 1

GENERAL INTRODUCTION ---------- 1
A REVIEW OF PREVIOUS WORK ---------- 1
QUESTIONS ADDRESSED IN THIS STUDY ---------- 4
RESEARCH OBJECTIVES ---------- 5
i: Reexamination of the Previously Named Species ---------- 5
ii: Description of New Genera and Species from North America ---------- 9
iii: Reconstruction of the Phylogeny and Classification ---------- 10
iv: Interpretation of Paleozoogeography of Osteoglossomorphs ---------- 12
METHODS ---------- 13
MATERIALS ---------- 14
LITERATURE CITED ---------- 16

Chapter 2

DESCRIPTION AND CLARIFICATION OF VALID †*PHAREODUS* SPECIES FROM NORTH AMERICA, WITH NOTES ON THE SYSTEMATICS OF †*PHAREOIDES QUEENSLANDICUS* (HILLS) ---------- 23
INTRODUCTION ---------- 23
Comparative Materials ---------- 24
SYSTEMATIC PALEONTOLOGY ---------- 26
Genus †*Phareodus* Leidy, 1873 ---------- 27
†*Phareodus encaustus* (Cope), 1870 ---------- 28
†*Phareodus testis* (Cope), 1877 ---------- 46
DISCUSSION ---------- 57
i. Two Valid North American †*Phareodus* Species ---------- 57
ii. Notes on Systematics of †*Phareoides queenslandicus* (Hills) ---------- 60
CONCLUSIONS ---------- 70
LITERATURE CITED ---------- 72
APPENDICES
2- I: Measurements of †*Phareodus encaustus* ---------- 76
2- II: Measurements of †*Phareodus testis* ---------- 77

Chapter 3

A LATE CRETACEOUS OSTEOGLOSSID FROM THE OLDMAN FORMATION OF ALBERTA, CANADA, AND ITS PHYLOGENETIC RELATIONSHIPS 78
INTRODUCTION 78
Geology 80
Comparative Materials 80
SYSTEMATIC PALEONTOLOGY 81
Genus †*Cretophareodus* gen. nov. 81
†*Cretophareodus alberticus* gen. et sp. nov. 84
DISCUSSION 87
CONCLUSIONS 95
LITERATURE CITED 96

APPENDIX

3- I: 28 characters used in the cladistic analysis 100

Chapter 4

THE DISCOVERY OF HETEROTIDINAE (OSTEOGLOSSIDAE) FROM THE PALEOCENE PASKAPOO FORMATION OF ALBERTA, CANADA 103
INTRODUCTION 103
Geology 104
Comparative Materials 105
SYSTEMATIC PALEONTOLOGY 105
Genus †*Joffrichthys* gen. nov. 106
†*Joffrichthys symmetroptera* gen. et sp. nov. 106
†*Joffrichthys* sp. 117
DISCUSSION 120
i. Taxonomic Setting of †*Joffrichthys* gen. nov. 120
ii. Comments on Early Evolution of Heterotinae 124
CONCLUSIONS 128
LITERATURE CITED 129

APPENDIX

4- I: 32 characters used in cladistic analysis 135

Chapter 5

NEW MATERIALS OF †*EOHIODON* FROM WESTERN NORTH AMERICA, WITH A TAXONOMIC REASSESSMENT OF HIODONTIDAE AND NOTOPTERIDAE 138

INTRODUCTION 138
  Comparative Materials 139
SYSTEMATIC PALEONTOLOGY 140
  Genus †*Eohiodon* Cavender, 1966 141
    †*Eohiodon woodruffi* Wilson, 1978 141
DISCUSSION 158
  i. Remarks on North American †*Eohiodon* Species 158
  ii. Reassessment of Taxonomic Position of Hiodontidae and Notopteridae 162
CONCLUSIONS 169
LITERATURE CITED 171
APPENDICES
  5- I: 65 characters used in cladistic analysis 175
  5-II: Measurements of the new specimens of †*Eohiodon woodruffi* 181

Chapter 6

AN EOCENE SPECIES OF *HIODON* FROM MONTANA, ITS PHYLOGENY, AND EVOLUTION OF THE POSTCRANIAL SKELETON IN HIODONTIDAE 182

INTRODUCTION 182
  Geology 184
  Comparative Materials 184
SYSTEMATIC PALEONTOLOGY 185
  Genus *Hiodon* Lesueur, 1818 186
    †*Hiodon consteniorum* sp. nov. 186
DISCUSSION 199
  i. Phylogenetic Relationships 199
  ii. Evolution of the Postcranial Skeleton in Hiodontidae 206
CONCLUSIONS 211
LITERATURE CITED 212
APPENDICES

6- I: 23 characters used in the cladistic analysis 217
6- II: Measurements of *Hiodon alosoides* (adult) from the North Saskatchewan River near Edmonton, Alberta 219
6-III: Measurements of *Hiodon alosoides* (juveniles) from Mamawi/Claire lakes, Alberta 220
6-IV: Measurements of *Hiodon tergisus* from the Red deer River, near Red deer, Alberta 221
6- V: Measurements of *Hiodon tergisus* from the North Saskatchewan River, near Edmonton, Alberta 222

Chapter 7

PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHIC HISTORY OF OSTEOGLOSSOMORPHA WITH EMPHASIS ON NORTH AMERICAN TAXA 223
- INTRODUCTION 223
  - Comparative Materials 225
- EXTRA-GROUP RELATIONSHIPS AND SYNAPOMORPHIES OF OSTEOGLOSSOMORPHA 225
  - i. Sister Group Relationship between Osteoglossomorpha and the Clade Clupeomorpha plus Euteleostei 230
  - ii. Monophyly of Osteoglossomorpha 232
- COMPOSITION AND INTERORDINAL RELATIONSHIPS OF OSTEOGLOSSOMORPHA 236
  - i. Stem-group Relationship between †Lycopteriformes and all Other Osteoglossomorphs 238
  - ii. Reconsideration of the Phylogeny of Hiodontiformes *sensu stricto* 240
  - iii. Synapomorphies of Osteoglossiformes 244
  - iv. Remarks on Definitions of Osteoglossoidei and Notopteroidei 245
- PHYLOGENY OF NORTH AMERICAN OSTEOGLOSSOMORPHS 250
  - i. Sister-group Relationships in Hiodontiformes *sensu stricto* 250
  - ii. Sister-group Relationships in Osteoglossoidei Lineage 253
  - iii. Reassessment of the Phylogeny of †*Ostariostoma* 257
- COMMENTS ON HISTORICAL BIOGEOGRAPHY OF OSTEOGLOSSOMORPHA 260
  - i. Previous Work on Osteoglossomorp Historical Biogeography 260

ii. Other Possible Interpretations of Osteoglossomorph Historical Biogeography ---------- 264
CONCLUSIONS ---------- 269
LITERATURE CITED ---------- 274
APPENDICES
7- I: 84 characters used in the cladistic analysis ---------- 284

LIST OF TABLES

TABLE 1-1 The previously described fossil osteoglossomorph fishes (valid species) from North America ---------- 3

TABLE 2-1 Ratio of depth to width of opercle of †*Phareodus encaustus* ------- 34

TABLE 2-2 Meristics of †*Phareodus encaustus* in AMNH and FMNH --------- 43

TABLE 2-3 Ratio of depth to width of opercle of †*Phareodus testis* ------------ 51

TABLE 2-4 **A:** Meristics of †*Phareodus testis* in collections of AMNH and FMNH ---------- 55

B: Meristics of †*Phareodus testis* in collections of FMNH, ROM, and UALVP ---------- 56

TABLE 2-5 Comparison of meristic characters among three †*Phareodus* species ---------- 67

TABLE 4-1 Data matrix showing the distribution of 32 characters and their states in the Osteoglossidae ---------- 123

TABLE 5-1 Meristics of †*Eohiodon rosei* ---------- 160

TABLE 5-2 Meristics of †*E. woodruffi* ---------- 161

TABLE 5-3 **A:** Data matrix showing the distribution of states of characters 1-33 in Osteoglossomorpha and selected out-groups --------------- 166

B: Data matrix showing the distribution of states of characters 34-65 in Osteoglossomorpha and selected out-groups -------------- 167

TABLE 6-1 Meristics of *Hiodon alosoides* listed in Appendices 6-II and 6-III ---------- 200

TABLE 6-2 Meristics of *Hiodon tergisus* listed in Appendices 6-IV and 6-V ---------- 201

TABLE 6-3 Comparison of some meristic characters among species in Hiodontiformes and †Lycopteriformes -------------------------------- 202

TABLE 7-1 **A:** Data Matrix showing the distribution of states of characters 1-21 of the 84 characters listed in Appendix 7-I ---------------------- 226

B: Data Matrix showing the distribution of states of characters 22-42 of the 84 characters listed in Appendix 7-I -------------------- 227

C: Data Matrix showing the distribution of states of characters 43-63 of the 84 characters listed in Appendix 7-I -------------------- 228

D: Data Matrix showing the distribution of states of characters 64-84 of the 84 characters listed in Appendix 7-I -------------------- 229

TABLE 7-2 The revised North American fossil osteoglossomorphs ------------- 252

LIST OF FIGURES

FIGURE 2- 1 FMNH PF14040, one of the new specimens of †*Phareodus encaustus* from the F-1 of Tinsky 1988 Quarry, Lincoln County of Wyoming. ---------- 25

FIGURE 2- 2 †*Phareodus encaustus*, showing the basic structure of the dorsal (**A**) and ventral (**B**) views of the neurocranium ---------- 31

FIGURE 2- 3 †*Phareodus encaustus*. Line drawing of the skull of FMNH PF14040. ---------- 35

FIGURE 2- 4 Lower and upper jaws of †*Phareodus encaustus* ---------- 36

FIGURE 2- 5 Some of the disarticulated bones of †*Phareodus encaustus*. ----- 39

FIGURE 2- 6 Restoration of the caudal skeleton of †*Phareodus* ---------- 45

FIGURE 2- 7 FMNH PF12411, one of the new specimens of †*Phareodus testis* from the F-2 of Tynsky 1986 Quarry, Lincoln County of Wyoming ---------- 48

FIGURE 2- 8 Photographs of the cranial skeleton of †*Phareodus testis* --------- 52

FIGURE 2- 9 Partial restoration of the cranial skeleton of †*Phareodus testis* based on UALVP 17658 ---------- 53

FIGURE 2-10 Partial restoration of the cranial skeleton of †*Phareodus queenslandicus* ---------- 63

FIGURE 2-11 Comparison of the posterior infraorbitals in †*Phareodus* --------- 65

FIGURE 2-12 Comparison of the jaws of †*Phareodus queenslandicus* with those of †*Phareodus encaustus* ---------- 68

FIGURE 2-13 Showing the hyomandibular of three †*Phareodus* species and the preopercle of †*Phareodus queenslandicus* ---------- 69

FIGURE 3-1 Map showing localities of the three North American Late Cretaceous teleosts referred to Osteoglossomorpha. --------------- 79

FIGURE 3-2 Holotype of †*Cretophareodus alberticus* gen. et sp. nov. (ROM 1323a).-- 82

FIGURE 3-3 Holotype of †*Cretophareodus alberticus* gen. et sp. nov. (ROM 1323b).--- 83

FIGURE 3-4 Partial restoration of the cranial skeleton of †*Cretophareodus alberticus* gen. et sp. nov. ----------------------- 85

FIGURE 3-5 Cladogram with data matrix, showing the possible phylogeny of †*Cretophareodus* -------------------------------------- 88

FIGURE 3-6 Four basic patterns of the opercle in Osteoglossomorpha --------- 90

FIGURE 3-7 Opercular series of †*Phareodus testis* ------------------------------- 92

FIGURE 3-8 Restoration of the cranial skeleton †*Singida jacksonoides* -------- 93

FIGURE 4-1 Photo of the holotype of †*Joffrichthys symmetroptera* gen. et sp. nov., taken from UALVP 23705a. ---------------------- 107

FIGURE 4-2 Two articulated specimens of †*Joffrichthys symmetroptera* gen. et sp. nov. --------------------------------------- 109

FIGURE 4-3 Parttial restoration of the cranial skeleton of †*Joffrichthys symmetroptera* gen. et sp. nov. --------------------------------------- 112

FIGURE 4-4 Disarticulated bones of †*Joffrichthys symmetroptera* gen. et sp. nov. -- 113

FIGURE 4-5 Restoration of the caudal skeleton of †*Joffrichthys symmetroptera* gen. et sp. nov. --------------------------------------- 116

FIGURE 4-6 †*Joffrichthys* sp., photo of UALVP 34770 ------------------------- 118

FIGURE 4-7 †*Joffrichthys* sp., restoration of the disarticulated cranial elements on UALVP 34770 -- 119

FIGURE 4-8 The only shortest tree generated by PAUP 3.1.1, showing the possible phylogenetic relationships among †*Joffrichthys* gen. nov. and other osteoglossids ------------------------------------- 122

FIGURE 4-9 Partial restoration of the cranial skeleton of †*Sinoglossus lushanensis*, modified from Su (1986) ------------------------------ 125

FIGURE 4-10 Cranial Skeleton of *Heterotis niloticus* and *Arapaima* gigas ----- 126

FIGURE 5-1 FMNH PF9882, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming -- 142

FIGURE 5-2 Enlargement of the cranial skeleton of FMNH PF12516, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming --------- 146

FIGURE 5-3 Some of the cranial skeleton of †*Eohiodon woodruffi* ------------- 149

FIGURE 5-4 Hyomandibular of †*Eohiodon* and *Hiodon* ------------------------- 151

FIGURE 5-5 Caudal skeleton of FMNH PF9878, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming -- 154

FIGURE 5-6 Photo of the caudal skeleton of FMNH PF12516, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming ---------------- 155

FIGURE 5-7 Preferred shortest tree showing the phylogeny of Hiodontidae and Notopteridae in Osteoglossomorpha --------------------------- 164

FIGURE 5-8 Strict consensus tree generated by PAUP 3.1.1 based on nine shortest trees -- 168

FIGURE 6-1 Map showing the fossil localities and the main part of the Flathead River system 183

FIGURE 6-2 Photo of †*Hiodon consteniorum* sp. nov. 187

FIGURE 6-3 Diagram showing the skull of the holotype of †*Hiodon consteniorum* sp. nov. 191

FIGURE 6-4 Caudal skeleton of the holotype of †*Hiodon consteniorum* sp. nov. 194

FIGURE 6-5 Caudal skeleton of the allotype of †*Hiodon consteniorum* sp. nov. 195

FIGURE 6-6 Caudal skeleton of the Recent *Hiodon alosoides* 196

FIGURE 6-7 Caudal skeleton of the Recent *Hiodon tergisus* 197

FIGURE 6-8 The most parsimonious tree generated by MacClade 3.04 and PAUP 3.1.1 from the cladistic analyses 203

FIGURE 6-9 Diagram showing the variation of the opercle in Hiodontiformes *sensu stricto* 205

FIGURE 10 Diagram showing the approximately proportional relationship between the increase in the number of vertebral centra and the enlargement of the anal fin in Hiodontidae, based on data of Table 6-3 209

FIGURE 7-1 Preferred shortest tree showing the monophyly of Osteoglossomorpha and the possible relationships among Osteoglossomorpha and other teleostean groups 231

FIGURE 7-2 Strict consensus tree generated by PAUP 3.1.1 based on 30 most pasimonious trees with 197 steps 233

FIGURE 7-3 50% majority rule consensus tree generated by PAUP 3.1.1 based on 30 most pasimonious trees with 197 steps 234

FIGURE 7-4 Triradiate dermosphenotic of *Hiodon alosoides* 243

FIGURE 7-5	Cranial skeleton of the selected osteoglossids	246
FIGURE 7-6	Infraorbitals of *Notopterus chitala* showing the infraorbital ledge	248
FIGURE 7-7	Revised restoration of the cranial and caudal skeleton of †*Ostariostoma wilseyi*	259
FIGURE 7-8	Diagram showing the hypothetical evolutionary history of Osteoglossomorpha	261
FIGURE 7-9	Map showing the modern geographic distribution of Osteoglossomorpha	263
FIGURE 7-10	Sketch map showing fossil evidence for the Early Cretaceous to early Late Cretaceous distribution of Osteoglossomorpha	265
FIGURE 7-11	Sketch map showing the Early Tertiary distribution of Osteoglossomorpha	267

ABBREVIATIONS

Institutional

AMNH	American Museum of Natural History, New York, USA
CMN	Canadian Museum of Nature, Ottawa, Canada
FMNH	Field Museum of Natural History, Chicago, USA
IVPP	Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China
KU	Museum of Natural History, The University of Kansas, Lawrence, Kansas, USA
PU	Princeton University, Princeton, New Jersey, USA
QM	Queensland Museum, Australia
ROM	Royal Ontario Museum, Toronto, Canada
UALVP	Laboratory for Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, Canada
UAMZ	Museum of Zoology, Department of Zoology, University of Alberta, Edmonton, Alberta, Canada
UF	University of Chicago Fossil Collection (Chicago Natural History Museum), Chicago, USA

Anatomical

ang	angular
angart	angulo-articular
angret	angulo-retroarticular
ao	antorbital
art	articular
asp	autosphenotic
bh	basihyal
boc	basioccipital
bpt.p	basipterygoid process
br	branchiostegals
br 1-8	1st to 8th branchiostegals

bs	basisphenoid
ch	ceratohyal
clt	cleithrum
cm	coronomeckelian
d.hh	dorsal hypohyal
den	dentary
dsp	dermosphnotic
ecp	ectopterygoid
enp	endopterygoid
eoc	exoccipital
ep	epural
epo	epiotic
esp	extrascapular (supratemporal)
fr	frontal
h1	1st hypural
h2	2nd hypural
h3-7	3rd to 7th hypurals
hm	hyomandibula
hpu2/3	haemal spine on 2nd or 3rd preural
io 1	1st infraorbital
io1-ao	fused antorbital and 1st infraorbital
io2	2nd infraorbital
io3	3rd infraorbital
io2-3	fused 2nd and 3rd infraorbitals
io4-5	fused 4th and 5th infraorbitals
iop	interopercle
mep	metapterygoid
mes	mesethmoid
mx	maxilla
na	nasal
npu1	neural spine on 1st preural
npu2	neural spine(s) on 2nd preural
nu1	neural spine on 1st ural
op	opercle
os	orbitosphnoid

pa	parietal
pas	parasphenoid
pclt	postcleithrum
ph	parhypural
pl	palatine
pmx	premaxilla
po	prootic
pop	preopercle
pt	posttemporal
pto	dermopterotic
pts	pterosphenoid
pu1	1st preural
pu2	2nd preural
qu	quadrate
rart	retroarticular
sclt	supracleithrum
sm	symplectic
soc	supraoccipital
sop	subopercle
ssc	supraorbital sensory canal
tf	temporal fenestra (temporal fossa or pre-epiotic fossa)
tpbh	tooth plate of the basihyal
u1	1st ural;
un1-3/4	1st to 3rd or 4th uroneurals
v.hh	ventral hypohyal
vo	vomer

Measurements (in mm)

AFBL	anal fin base length
BD	body depth
CPD	caudal peduncle depth
CPL	caudal peduncle length
DFBL	dorsal fin base length

FL	fork length
HD	head depth
HL	head length
OD	opercular depth
OW	opercular width
PAL	preanal length
PDL	predorsal length
PPL	prepectoral length
PVL	prepelvic length
SL	standard length

Meristics

AFR	principal anal fin rays
AP	anal pterygiophores
BR	branchiostegals
CFR	principal caudal fin rays
CV	caudal vertebrae
DFR	principal dorsal fin rays
DP	dorsal pterygiophores
EP	epural
H	hypurals
PFR	pectoral fin rays
PCV	precaudal vertebrae
SN	supraneurals
TV	total vertebrae
UN	uroneurals
VFR	pelvic fin rays.

Chapter 1

GENERAL INTRODUCTION

Osteoglossomorpha are a group of teleostean fishes that are most closely related to the clade Clupeomorpha plus Euteleostei (see Figs. 7-1). With the exception of *Hiodon*, which is the only representative of this fish group living in North America, all the other extant genera in Osteoglossomorpha survive in the tropical or subtropical fresh waters of South America (*Arapaima*, *Osteoglossum*), Australia (*Scleropages*), Southeast Asia (*Scleropages*), Africa (*Heterotis*, *Pantodon*, *Xenomystus*, *Papyrocranus*, and all Mormyroidea), and southern India (*Notopterus*) (Nelson, 1994).

Previous discoveries of fossil osteoglossomorphs in North America may be referred to some of the major lineages of Osteoglossomorpha: †*Eohiodon* for Hiodontidae, †*Phareodus* for Osteoglossidae, and †*Ostariostoma* for Notopteroidei. These discoveries have been extended by new materials from the Upper Cretaceous to Lower Tertiary of Alberta, British Columbia, and Montana discussed in this thesis, representing all the major osteoglossomorph clades. Since no other continents are known to have fossil records for so many main lineages of this fish group, a comprehensive study of the North American osteoglossomorphs promises to be particularly important for reconstructing the phylogeny and interpreting the historical biogeography of the Osteoglossomorpha, and the role of osteoglossomorphs in the evolutionary history of the North American freshwater fish fauna.

Therefore, the focus of this thesis is to clarify the phylogenetic relationships among the osteoglossomorphs from North America relative to those from other continents, on the basis of a reexamination of the previously named species and the description and comparative study of the new taxa.

A REVIEW OF PREVIOUS WORK

The study of North American fossil osteoglossomorphs was pioneered by Cope (1870) and Leidy (1873) in the middle of the nineteenth century. The first two fossil osteoglossomorph fishes recorded in North America were †*Phareodus encaustus* (Cope) 1872 and †*Phareodus testis* (Cope) 1873 (Table 1-1) from the Eocene Green River Formation of Wyoming. These records were added to in 1966 when Cavender transferred Hussakof's †"*Leuciscus*" *rosei* from the genus "*Leuciscus*" and gave it the generic name †*Eohiodon.*

†"*Leuciscus*" *rosei* was collected by Rose in 1912 from the Tranquille Bed at Kamloops Lake, British Columbia and originally assigned to the family Cyprinidae by Hussakof (1916). In 1966, Cavender made a detailed investigation of †"*Leuciscus*" *rosei* by redescribing the type specimens and comparing their characters with those of the Recent North American *Hiodon*. He renamed it †*Eohiodon rosei*, and grouped it with *Hiodon* in the family Hiodontidae. Cavender's establishment of †*Eohiodon* has been followed by all later paleoichthyologists studying osteoglossomorph fishes (Greenwood, 1966, 1970; Zhang and Zhou, 1976; Wilson, 1977, 1978, 1980; Wilson and Williams, 1993; Taverne, 1977, 1978, 1979; Grande, 1979, 1984, 1985a, 1989; Li, 1987; Shen, 1989; Jin, 1991). Besides †*Eohiodon rosei*, species presently grouped in this genus are: †*E. woodruffi* Wilson 1978, occurring in the middle Eocene fresh water tuffaceous shales of the lower Tom Thumb Tuff Member and the middle member of the Klondike Mountain Formation, near Republic, Washington, and the middle Eocene strata at Horsefly, B. C.; and †*E. falcatus* Grande 1979 from the Green River Formation of the Eocene Fossil Lake, Wyoming. Shen (1989) named another †*Eohiodon* species (†*E. shuyangensis*) based on one specimen from the Eocene deposits of Jiangsu, eastern China. The validity of that species is doubtful (it might be a juvenile †*Phareodus,* pers. obs.). Additional reports of North American fossil hiodontids have been made on the basis of scales from the late Eocene or Oligocene Clarno Formation of north-central Oregon, the Oligocene Grant shales of southwestern Montana (see Cavender, 1968), and the Paleocene Paskapoo Formation of Alberta (Wilson, 1980). Articulated fossil hiodontids have also been reported from the Palaeogene of Mongolia (Sytchevskaya, 1986) and the upper Lower Cretaceous to Upper Cretaceous of northeastern China (Zhang and Zhou, 1976; Li, 1987).

The study of †*Phareodus* has also neen renewed since 1960. Greenwood (1966) found similarities between the caudal skeleton of †*Phareodus* and those of *Scleropages* and *Heterotis*. Roellig (1967) reviewed the osteology of the Osteoglossidae, and revised the generic diagnosis for †*Phareodus*, recognizing four species including †*Phareodus queenslandicus* (Hills, 1934). Taverne (1973, 1974, 1977, 1978, 1979) examined most of the genera grouped in Osteoglossomorpha. He mentioned the close similarity

TABLE 1-1: The previously described fossil osteoglossomorph fishes (valid species) from North America.

DESCRIBED SPECIES	TIME NAMED	LOCATION	STRATIGRAPHIC DISTRIBUTION
†*Phareodus encaustus*	(Cope) 1872	Fossil Lake	Eocene, Green River Formation
†*Phareodus testis*	(Cope) 1873	Fossil Lake	Eocene, Green River Formation
†*Eohiodon rosei*	(Hussakof) 1916	Kamloops	Eocene, Tranquille Beds
†*Eohiodon woodruffi*	Wilson 1978	Republic	Middle Eocene, Klondike Mountain Formation
†*Eohiodon falcatus*	Grande 1979	Fossil Lake	Eocene, Green River Formation
†*Chandlerichthys strickeri*	Grande 1987	Arctic Slope	Albian or Cenomanian, Chandler Formation
†*Ostariostoma wilseyi*	Schaeffer 1949	Raw Liver Creek	Upper Cretaceous, Livingston Formation

between †*Phareodus* and †*Brychaetus* (Woodward, 1901) and renamed †*Phareodus queenslandicus* as †*Phareoides queenslandicus.* Grande (1984) briefly summarized the history of the study of †*Phareodus*; he believed †*Phareodus encaustus* and †*P. testis* to be valid species from the Green River Formation.

The first definite report of a North American Cretaceous osteoglossomorph fish is that of †*Chandlerichthys strickeri* Grande, 1986, described on two incomplete specimens from fresh water deposits of the Killik Tongue, Chandler Formation, Nanushauk Group, Arctic Slope of northern Alaska.

Grande and Cavender (1991) recently discussed the possible osteoglossomorph relationship of †*Ostariostoma.* This genus was first described by Schaeffer (1949), on a single specimen from the Upper Cretaceous or lower Paleocene freshwater deposits of the Livingston Formation in Montana, and assigned to the superfamily Clupeoidea.

Attempts to reconstruct the historical biogeography of osteoglossomorph fishes in North America have been made by Nelson (1969), Greenwood (1970), Zhang and Zhou (1976), Patterson (1981a), Grande (1986, 1989), Li (1987), and Wilson and Williams (1993).

It is, however, notable that the previous studies on North American fossil osteoglossomorphs have mainly concentrated on the description of genera and species (Leidy, 1873; Cope, 1873, 1877a-b, 1878, 1883; Thorpe, 1938; Cavender, 1966; Wilson, 1977, 1978; Grande, 1979, 1984, 1986). Little research has been done on phylogeny and biogeography of the North American osteoglossomorphs. Moreover, it remains unclear whether the North American †*Phareodus* species can be referred to the genus known in northeast Australia (Hills, 1934) and central China (East Asia) (Song, 1990, pers. comm.; Chang and Zhou, 1993), and which two species included in the Eocene †*Eohiodon* are most closely related with each other.

QUESTIONS ADDRESSED IN THIS STUDY

As mentioned above, the phylogeny of the previously described osteoglossomorphs from North America is not well understood. No effort has yet been made to determine the sister-group relationships in †*Eohiodon.* No detailed investigation has been carried on the differences between †*Phareodus encaustus* and †*P. testis*, or on their possible phylogenetic position in the family Osteoglossidae. Until now, †*Chandlerichthys* and †*Ostariostoma* have been only tentatively included in Osteoglossomorpha; their relationships to other osteoglossomorphs are not clear. Finally, clarification is needed about how many named species are valid taxa, and about the new taxa that may be named on the undescribed materials from Alberta, British Columbia, and Montana.

Following from these outstanding issues, there are eight basic questions to be addressed in this research:

(1) Is †*Phareodus encaustus* most closely related to †*Phareodus testis*?

(2) Might †*Eohiodon falcatus* be synonymous with †*E. woodruffi*?

(3) Does the new hiodontid material from the upper Eocene of Montana represent a fossil species of †*Eohiodon* or of *Hiodon*?

(4) What groups are represented by the discoveries from the Upper Cretaceous Oldman Formation and the Paleocene Paskapoo Formation of Alberta?

(5) Are the Osteoglossomorpha a monophyletic group?

(6) How to evaluate the relationships among †Lycopteridae, Hiodontidae, and Notopteridae?

(7) To which of the lineages of Osteoglossomorpha, if any, is †*Ostariostoma* most closely related?

(8) What historical biogeographical patterns may be suggested by a more precise phylogeny of Osteoglossomorpha?

RESEARCH OBJECTIVES

As a comprehensive study of the North American fossil osteoglossomorphs, this thesis is concerned primarily with three aspects: (1) morphological comparison of North American fossil osteoglossomorphs with their relatives in other continents, (2) phylogenetic analysis of osteoglossomorph fishes, both fossil and Recent, based on the new information indicated by the North American materials, and (3) interpretation of the historical biogeography of Osteoglossomorpha with special reference to the origin of North American taxa.

Four research projects have been carried out since 1991.

i: Reexamination of the Previously Named Species

All of the previously named species listed in Table 1-1 have been reviewed. A detailed description has been given for †*Phareodus* species based on new specimens collected from the Green River Formation, Wyoming. The results of my study indicate that †*Phareodus encaustus* and †*P. testis* are valid species (see Chapter 2), in agreement with Grande (1984). A comparison of †*Phareoides queenslandicus* (Hills) 1934 with †*Phareodus encaustus* does not support the validity of †*Phareoides* (Taverne, 1973), but confirms that †*Phareodus queenslandicus* (Hills, 1934) is a valid species (Chapter 2).

Some supplementary description and emendations have been made for †*Eohiodon woodruffi*. The investigation of new materials of †*Eohiodon woodruffi* from the Eocene Horsefly Beds of British Columbia and new materials of †*Eohiodon falcatus* from the Green River Formation of Wyoming strongly suggests that †*Eohiodon falcatus* is synonymous with †*Eohiodon woodruffi* (Chapter 5).

This reexamination has also resulted in a relatively clear understanding of the following questionable characters:

1. Temporal fossa– Gaudant (1968) first noticed the presence of a "temporal fossa" in †Lycopteridae. My investigation indicates that four types of so-called temporal fossae can be identified in osteoglossomorphs (pers. obs.; also see Ridewood, 1904, 1905; Gosline, 1960; Greenwood, 1966, 1970, 1973; Roellig, 1967, 1974; Nelson, 1969, 1973b; Kershaw, 1976; and Taverne, 1977, 1978, 1979). The temporal fossa is bounded by the parietal, pterotic, and epiotic in hiodontids (where it is covered by the supratemporal), in pantodontids, and in notopterids. This type of temporal fossa is exactly the same as the so-called "pre-epiotic fossa" in both the position and composition (see Patterson, 1970), and is also present in Clupeomorpha (Grande, 1985b).

In most osteoglossids, including †*Phareodus*, the fossa is mainly bounded by the pterotic and epiotic. A similar fossa in notopterids is surrounded by the pterotic, epiotic and exoccipital. In *Arapaima*, the intercalar participates in the construction of the fossa.

However, it is still an open question whether the temporal fossae in hiodontids, osteoglossids and notopterids are homologous or not.

2. Articulation facet on lower jaw for quadrate– Nelson (1973a-b) discussed the phylogenetic significance of the articulation facet for the quadrate in teleosts. He defined three basic types of quadrate facet in osteoglossomorphs. †*Phareodus* has a facet only on one cartilage-replacement bone (articular). *Heterotis* develops a facet on two such bones (articular and retroarticular). A facet constructed by one cartilage-replacement bone (articular) and one compound bone (angulo-retroarticular) is seen in *Hiodon* and its close relatives. According to Wilson (pers. comm.), a three-part facet may be also present in †*Joffrichthys* gen. nov., a new fossil osteoglossid from the Paleocene Paskapoo Formation of central Alberta, Canada. The facet in juveniles of *Hiodon* may be different from the facet in adults because the retroarticular is not fused with the angular and it does not participate in the construction of the facet before maturity. This means that this feature may be less important for determining the phylogenetic relationships of the members in Osteoglossomorpha than was expected.

3. Basipterygoid processes of parasphenoid– According to Ridewood (1904, 1905), Greenwood et al. (1966), Kershaw (1976), and Taverne (1977, 1978, 1979), a pair of basipterygoid processes on the parasphenoid is present in Pantodontidae and Osteoglossidae but absent in Hiodontidae, Notopteridae and Mormyridae. It is also present in †*Phareodus* (pers. obs.; also see Taverne 1978) and †*Singida,* but absent in †*Eohiodon* and in other fossil hiodontids found in East Asia. So-called basipterygoid processes are developed in basal teleosts such as †*Pholidophorus* (Patterson 1975a), †*Huashia* (Chang and Chou, 1977), and †*Kuntulunia* (Liu et al., 1982). This suggests that the presence of basipterygoid process on the parasphenoid is a plesiomorphic state, while the absence of the process in some osteoglossomorphs, including †*Lycoptera* and †*Yanbiania*, is possibly secondary.

4. Distribution pattern of cephalic sensory canals– The arrangement of the cephalic sensory canals differ among the genera in Osteoglossomorpha. This is particularly shown by the supraorbital canal that may end in the parietals (e.g., †*Lycoptera*) or in the frontals (e.g., *Hiodon*, †*Eohiodon*, †*Phareodus*, *Osteoglossum*). The cephalic sensory canal in the preopercle may extend along the anterior (orbital) margin of the bone (e.g., hiodontids and *Heterotis*), or may pass through the middle of this bone (e.g., *Osteoglossum*, *Scleropages*, †*Phareodus*, and †*Brychaetus*). The number and position of the branches given off from the preopercular canal seems to be regular in different families of Osteoglossomorpha. In Osteoglossidae, the preoperculo-mandibular canal opening in a groove on the horizontal arm of the preopercle has been found to be the most important synapomorphy shared by all the members in the subfamily Osteoglossinae (See Chapter 2, 4).

5. Teeth on parasphenoid– Three states of this character can be seen in Osteoglossomorpha. In all of the hiodontiforms teeth on the parasphenoid are present along the whole length of the ventral side. This state is here considered to be plesiomorphic. In the Recent *Heterotis* and the fossil †*Singida*, teeth are absent from the parasphenoid. This may be an apomorphic state. An intermediate condition of this character is seen in †*Phareodus*, *Osteoglossum*, and *Scleropages*, in which the parasphenoid bears teeth on its posterior part ventro-medial to the basipterygoid process.

6. Opercle– Four basic types of opercle may be identified in Osteoglossomorpha (Chapter 3: Fig. 3-6). A subrectangular opercle that may have a protruding upper posterior border and an acute postero-dorsal projection (e.g. *Hiodon*) is considered to be an important synapomorphy of Hiodontidae (Chapter 5-6), and a subsemicircular opercle to be a synapomorphy of Osteoglossinae (Chapter 2-3).

7. Frontal– In most osteoglossomorphs, the frontal is anteriorly narrower or only slightly broader than it is posteriorly. †*Phareodus* and †*Brychaetus* share frontals that are anteriorly twice as broad as posteriorly. The frontal in the new genus †*Cretophareodus* resembles that in †*Phareodus* and †*Brychaetus* (Chapter 3). This second state is here considered to be synapomorphic for some Osteoglossomorpha.

8. Fusion of antorbital with first infraorbital– This character state is seen only in †*Sinoglossus*, *Heterotis*, and *Arapaima*. It is considered to be the most important synapomorphy linking these three genera.

9. "Cheek wall"– In †*Sinoglossus*, *Heterotis*, and *Arapaima*, the first and second infraorbitals are greatly enlarged to form a "cheek wall" together with the third infraorbital. Differing from the "infraorbital ledge" in notopterids (Greenwood et al., 1966), the "cheek wall" in the above three genera covers all the area from the antorbital to the anterior edge of the preopercle.

10. Postcranial skeleton– Characters from the postcranial skeleton have been used for describing and comparing differences among osteoglossomorph fishes mainly at the level of species. For the lineages that have relatively complete fossil records, such as Hiodontidae (Chapter 5-6), postcranial skeletal characters have been shown to be important for tracing the evolutionary history of the lineages (Chapter 6). A detailed cladistic analysis of postcranial characters in Osteoglossomorpha has clarified several evolutionary trends, including the fusion of the upper hypurals and the loss of the uroneurals, in this teleostean group.

11. Number of pelvic fin rays– Most of the genera in Osteoglossomorpha, including †*Lycoptera* and †*Phareodus,* have 4-6 pelvic fin rays. However, this character state is even more fixed in Hiodontidae; all of the genera in this family (*Hiodon*, †*Eohiodon*, †*Plesiolycoptera*, and †*Yanbiania*) have seven rays in each pelvic fin. Therefore, a seven-rayed pelvic fin is considered to be a synapomorphy of Hiodontidae.

12. Reticulated scales– Reticulated scales were thought to be diagnostic of Osteoglossiformes (Taverne, 1979). However, scales found so far in Cretaceous osteoglossiforms, including †*Laeliichthys* (Santos, 1985) from South America and the new genus †*Cretophareodus* from the Oldman Formation of southeastern Alberta, Canada (Chapter 3), are cycloid with no reticulations. The scales of †*Singida* and the Paleocene new heterotidine †*Joffrichthys* are also lacking reticulations. The Eocene

†*Phareodus* and †*Sinoglossus* (Su, 1986) are the only two fossil genera having reticulated scales. This indicates that reticulated scales seen in the Recent osteoglossomorphs might be a novelty resulting from convergence since the Paleogene.

13. Relative position of dorsal fin to anal fin in †*Phareodus*– Externally, there is a tendency for the dorsal fin to move posteriorly during the development from juvenile to adult in †*Phareodus* (in terms of the predorsal and preanal lengths). As shown in Appendices 2-I and 2-II, when the individual fish has a value of SL≤ 100mm, the dorsal fin is oposite the anal fin. However, on the largest specimen (e.g., FMNH PF14040), the beginning of the dorsal fin is 55mm posterior to the beginning of the anal fin.

Internally, both the anteriormost dorsal pterygiophore and the anteriormost anal pterygiophore are connected with the same vertebral centrum, the first caudal vertebrae (=the last preural) via its neural and the haemal spines in both the juvenile and the adult. This means that both the dorsal and anal fins begin internally from the same vertebral centrum. Therefore the relative position of the dorsal fin to the anal fin is taxonomically unimportant in the classification of the †*Phareodus* species.

ii: Description of New Genera and Species from North America

This study has resulted in the establishment of two new genera of Osteoglossidae (chapters 3 and 4) and one new species of *Hiodon* in the Hiodontidae (Chapter 6).

1. †*Cretophareodus* gen. nov.– This new genus is established on the material from the Upper Cretaceous Oldman Formation at Steveville of Alberta (Chapter 3). It differs from all other genera in the subfamily Osteoglossinae in having the corner of the mouth lying at the level of the posterior margin of the orbit, the articulation facet for the quadrate on the articular and retroarticular, the pectoral fin consisting of only six rays, the dorsal fin larger than the anal fin, subcycloid scales with fine growth lines interrupted by both the basal and apical radii, and depth to width ratio of the opercle 1.72. Based on the subsemicircular opercle, the short horizontal arm of the preopercle extending anteriorly only to the level of the postero-ventral corner of the third infraorbital, the preoperculo-mandibular canal on the horizontal arm of the preopercle opening in a groove, and the strong first pectoral fin ray, this Late Cretaceous osteoglossid is considered to be most closely related to the Eocene †*Phareodus* and †*Brychaetus* in Osteoglossinae.

2. †*Joffrichthys* gen. nov.– This genus is named on three articulated specimens and some disarticulated elements recently collected from the Paleocene Paskapoo Formation at the Joffre Bridge locality, southern Alberta (Chapter 4). This Paleocene member of the Heterotidinae differs from the Recent genera in having small pectoral fins, both the dorsal and anal fins consisting of the same number (24) of principal rays, caudal vertebrae "H"-shaped in lateral view, and scales cycloid, with nearly central focus, and with no reticulation. Taxonomic placement of this new genus in the Heterotidinae is based on the oval opercle, the lengthened horizontal arm of the preopercle, the anteriorly located mouth corner (anterior to the orbit), the three branches of the preoperculo-mandibular canal on the horizontal arm of the preopercle, and the short distance between the small pelvic fin and the large anal fin.

Disarticulated materials from the Paleocene Paskapoo Formation at the Smoky Tower locality, northwestern Alberta, have also been included in this study. They may represent a different species of †*Joffrichthys* gen. nov. (Chapter 4), but remain unnamed in this thesis.

3. †*Hiodon consteniorum* sp. nov.– This is the first known fossil species of *Hiodon,* named on two well-preserved specimens from the upper Eocene Kishenehn Formation at the Tunnel Creek locality, Montana (Chapter 6). This fossil species of *Hiodon* is distinguishable from the two Recent species in having a relatively deeper and narrower mid-dorsal concavity on the premaxilla, a posteriorly more expanded maxilla extending not beyond the posterior 1/3 of the orbit, a longer basihyal tooth plate (more than 3/5 versus about 1/2 as long as the lower jaw in Recent species), fewer vertebrae (52-53 versus 55-61 or 63 in the Recent species), and fewer anal pterygiophores (20 versus 27-36 in the Recent species). It is also different from the two Recent species in some ratios (see Chapter 6).

iii: Reconstruction of the Phylogeny and Classification

This study confirms that the Osteoglossomorpha are a monophyletic group that is the sister to the Clupeomorpha plus Euteleostei (Chapter 7). What follows are the main points about the phylogeny of the North American fossil and extant osteoglossomorphs.

1. The establishment of the relationship between the Mesozoic †*Lycoptera* and the Recent *Hiodon* (Greenwood, 1970) was a significant advance in the study of the lycopterid lineage, but it has not solved the problem of the relationship between *Hiodon* and other Recent osteoglossomorph genera. For many years, ichthyologists (Regan, 1909; Greenwood, 1963, 1973; Greenwood et al., 1966; Nelson, 1984) have mistakenly linked *Hiodon* with African and southern Indian notopterids, grouping them in the same suborder Notopteroidei mainly on the basis of the presence of a "swimbladder-ear connection." However, a "swimbladder-ear connection" has also been proved to exist in other genera of Osteoglossomorpha (Greenwood 1966, 1973; Grande, 1985). Moreover, in skeletal characters, hiodontids and notopterids share almost no common features except those plesiomorphies shared by all other osteoglossomorphs. These facts suggest that the so-called relationship between the Recent *Hiodon* and notopterids needs to be reassessed. My suggestions on clarifying some of these questions are summarized in Chapter 5.

2. Opinion seems unanimous about the relationship between North American †*Phareodus* and the southern hemispheric osteoglossids. However, the main character on which †*Phareodus* was grouped in Osteoglossidae is its reticulated scales. Among characters that have been neglected are those from the cranial and caudal skeleton. A cranial skeletal comparison of †*Phareodus* with †*Cretophareodus* gen. nov. and †*Brychaetus* suggests that these three genera are phylogenetically more closely related with each other than they are to the others in Osteoglossomorpha (see chapters 3 and 7). Considering the caudal skeleton, Cavender (1966) and Greenwood (1966) noted only the primitive aspects of the caudal skeleton of †*Phareodus* in comparison with the caudal skeleton in other Recent osteoglossids. My reexamination of the caudal skeleton of †*Phareodus* brought to mind the caudal skeleton of the Cretaceous †*Asiatolepis* Takai, 1943 (see Li, 1987: fig. 5). The two caudal skeletons have the following characters in common: uroneurals are absent in both †*Phareodus* and †*Asiatolepis*, the first ural centrum has two neural spines followed posteriorly by one or two epurals, and six hypurals support 17 principal caudal fin rays. I believe some phylogenetic information could be gleaned from the caudal skeleton of †*Phareodus*. Nelson (1969), moreover, mentioned the close similarity between †*Phareodus* and †*Musperia* (Sanders, 1934) and presumed that "they may together represent an early side branch" of Osteoglossiformes. Indeed, my study suggests that †*Musperia* is possibly synonymous with †*Phareodus* (Chapter 3).

3. A reassessment of the phylogeny of †*Ostariostoma* indicates that this North American genus may represent an early lineage of Mormyroidea (see Chapter 7). Further investigation of †*Ostariostoma* suggests that it might share a common ancestor with the western European †*Thaumaturus*.

4. In addition, the osteoglossomorph relationship of †*Chandlerichthys* is also reassessed (see Chapter 7). It might prove to be more closely related to the South American †*Laeliichthys* than to other genera in Osteoglossidae. However, the poor preservation of the material makes it impossible to further discuss its phylogeny.

5. A revised phylogeny of osteoglossomorph fishes is proposed in Chapter 7; it is hoped that this will provide a framework for further discussion of the evolution of the Osteoglossomorpha.

iv: Interpretation of Paleozoogeography of Osteoglossomorphs

Two models, vicariance and dispersal (Croizat, 1958, 1964, 1982; Platnick and Nelson, 1978; Nelson et al., 1980, 1981; Patterson, 1981; and Grande, 1985), are applied in this thesis. Hypotheses on the historical biogeography of osteoglossomorphs from North America are summarized in Chapter 7. I agree with Grande (1985a) as regards the functions of fossil evidence in paleobiogeography. Both cladistic dispersal and cladistic vicariance models (Nelson, 1969, Platnick and Nelson, 1978) might explain the establishment of the Recent distribution patterns of Osteoglossomorpha.

Early representatives of Osteoglossomorpha have been reported from the Upper Jurassic to Lower Cretaceous of East Asia (†*Lycoptera* Müller, 1847; †*Yanbiania*, †*Tanichthys* Jin, 1991), the Aptian of South America (†*Laeliichthys*), the Albian to Cenomanian (†*Chandlerichthys*) and Campanian to Maastrichtian (†*Cretophareodus* gen. nov. and †*Ostariostoma*) of North America, the Cenomanian of Africa (†*Kipalaichthys*, see Taverne, 1979), and it is suggested here, possibly from the Lower Cretaceous of Australia (†*Koonwarria* Waldman,1971). These genera seem unlikely to be the earliest lineages of Osteoglossomorpha because they already share many of the synapomorphies that distinguish subgroups within Osteoglossomorpha. Moreover, they are found on most of the main land masses in the process of splitting of Laurasia and Gondwana.

A new hypothesis about osteoglossomorph historical biogeography is proposed in Chapter 7. I suggest that the earliest ancestors of Osteoglossomorpha might have completed their early development in Pangaea by the Middle to the Late Jurassic. Fossil evidence from the mid-Cretaceous and Lower Tertiary of North America, East Asia, Africa, South America, and Australia, and from the Lower Tertiary of Europe (Woodward, 1901; Gaudant, 1981, 1988; Micklich, 1992) and India (Hora, 1938), indicates that the Recent transoceanic distribution of Osteoglossomorpha could have resulted from three major vicariance events: (1) the split of Pangaea into Laurasia and Gondwana between the Late Jurassic and Early Cretaceous; (2) the split of Gondwana, the most important event in osteoglossomorph history and related to the formation of the southern Atlantic and Indian oceans between the Late Jurassic and early Tertiary, producing the transoceanic distribution pattern of the order Osteoglossiformes; and (3) the separation between North America and Eurasia between the Late Cretaceous and the

Recent, which is compatible with ideas of Grande (1989) and Wilson and Williams (1993) in explaining the historical biogeography of the Hiodontiformes. These three vicariance events are approximately consistent with three major divisions in the ancestral osteoglossomorph lineages since the Late Jurassic (see Chapter 7). Further investigation may corroborate the idea that the early evolution of Notopteroidei occurred first in Euramerica based on the possible sister-group relationship of †*Ostariostoma* and †*Thaumaturus*, while the Recent southern distribution of this lineage might be secondary.

METHODS

Terminology– Terms used for general description follow Wilson (1977), Patterson and Rosen (1977), Grande (1984), Li (1987), Grande and Cavender (1991), and Wilson and Williams (1991); for palatoquadrate series, terms follow Arratia and Schultze (1991); for caudal skeleton, terms mainly follow Arratia (1991), Arratia and Schultze (1992), Schultze and Arratia (1988, 1989).

Biogeographic terminology follows Nelson (1975, 1976, 1978), Platnick and Nelson (1978), Nelson and Platnick (1979, 1980, 1981), Brundin (1981), Patterson (1981a-b), Croizat (1981, 1982), Croizat et al. (1974), Grande (1985a), and Bänärescu (1990).

Phylogenetic Analyses– Cladistic analyses were carried out with the aid of PAUP 3.1.1 (Swofford 1993) and MacClade 3.04 (Maddison and Maddison 1992). Characters used for cladistic analysis are mainly from the skeletal system that are observable in both fossil and Recent taxa. They are listed in the appendices following each of the chapters and represented by numbers in the text. All of the characters are unordered and equally weighted in analyses. Each of the character states of a given character is placed in square brackets following the number representing the character (e.g., 10[1] is character state 1 of character 10). Missing states are coded by question marks in the data matrix. Characters are considered to be highly homoplastic if their consistency index (CI) is smaller than 0.5 and slightly homoplastic if they have a CI equal or greater than 0.5 but less than 1.

I chose †*Leptolepis coryphaenoides,* †*Tharsis dubius,* †*Allothrissops* (see Nybelin, 1974), some typical ichthyodectiforms (Patterson and Rosen, 1977; Maisey, 1991), Recent elopomorphs, and selected primitive clupeomorphs and euteleosts for the purpose of comparison. These fishes have been used to test whether a character shown by fossil osteoglossomorphs is apomorphic (derived) or plesiomorphic (primitive).

Phylogenetic relationships are established based on shared derived character states, including some of the slightly homoplastic ones. Monophyletic groups are defined in terms of synapomorphies (Hennig, 1966) shared by all the members in the taxon.

Preparation of Specimens– Fossil specimens were mechanically prepared. Comparative Recent fishes consist of dried skeletons, specimens fixed in formalin and preserved in alcohol or cleared and stained with alizarin.

Measurements and Counts– Data for measurements and counts are from complete fossil specimens and Recent fishes; they were made following Hubbs and Lagler (1964).

Statistical Data Analysis– A number of measurements and meristics are selected for statistical analyses using the StatView program (Feldman et al., 1991).

MATERIALS

Materials involved in this thesis are referred to the following taxa.

†Lycopteriformes– †Lycopteridae: *†Lycoptera davidi* (Sauvage), *†Tongxinichthys microdus* Ma.

Hiodontiformes– Hiodontidae: *Hiodon tergisus* Lesueur, *Hiodon alosoides* (Rafinesque), *†Hiodon consteniorum* sp. nov., *†Eohiodon rosei* (Hussakof), *†Eohiodon woodruffi* Wilson, *†Eohiodon falcatus* Grande, *†Yanbiania wangqingica* Li, and *†Plesiolycoptera daqingensis* Chang and Chou.

Osteoglossiformes– Osteoglossidae: *Osteoglossum bicirrosum* (Vandelli), *Osteoglossum ferreirai* Kanazawa, *†Phareodus testis* (Cope), *†Phareodus encaustus* (Cope), *Arapaima gigas* (Cuvier), *†Sinoglossus lushanensis* Su.

Pantodontidae: *Pantodon buchholsi* Peters.

Notopteridae: *Notopterus chitali* Hamilton, *Xenomystus nigri* Günther.

Mormyridae: *Gymnarchus* Cuvier.

Gonorhynchiformes– Chanidae: *Chanos chanos* (Forkal).

Salmoniformes– Salmonidae: *Coregonus* Linnaeus.

Osmeridae: *Hypomesus* Gill, *Thaleichthys* Girard.

The UALVP has a collection of osteoglossomorph specimens mainly from the following localities: Split Rock, Falkland, and Horsefly River (Kamloops Group) in British Columbia; Joffre Bridge and Smoky Tower of the Paskapoo Formation in Alberta; Oldman Formation in Dinosaur Provincial Park of southern Alberta; Julian

Quarry, Slab Site (Fossil Butte) and Tynsky Quarry of the Green River Formation in Wyoming; and Tunnel Creek of the Kishenehn Formation in Montana.

Specimens deposited in the collections of the AMNH, CMN, FMNH, IVPP, PU, QMA, ROM, TMP, UAMZ, and UF are also used for this project.

All exclusively fossil taxa are marked with daggers (†) preceding their names throughout this thesis.

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Chapter 2

DESCRIPTION AND CLARIFICATION OF VALID †*PHAREODUS* SPECIES FROM NORTH AMERICA, WITH NOTES ON THE SYSTEMATICS OF †*PHAREOIDES QUEENSLANDICUS* (HILLS)*

INTRODUCTION

†*Phareodus* Leidy (1873) was the first fossil member of the Osteoglossomorpha recorded in North America. It was initially named on disarticulated mandibular elements and trunk scales collected from the Green River Formation of Wyoming. Those materials were originally referred to *Osteoglossum*, a Recent genus living in the fresh waters of South America (Cope, 1870). In 1877, Cope coined the name †*Dapedoglossus* for another fossil genus of Osteoglossidae based on the Green River materials similar to Leidy's †*Phareodus.* Some 60 years later, Thorpe (1938) abolished Cope's †*Dapedoglossus* because of its synonymy with Leidy's †*Phareodus.* Among more modern paleoichthyologists, †*Phareodus* is commonly accepted and used (Cavender, 1966; Greenwood, 1966; Roellig, 1967; Taverne, 1977, 1978, 1979; Grande, 1984, 1985).

In North America †*Phareodus* has been found so far only in the Fossil Butte Member of the Green River Formation of Lincoln County, Wyoming, USA. It is, however, interesting that fully five species were once included in this genus (see the synonymies for †*Phareodus encaustus* and †*Phareodus testis* in this chapter). Roellig (1967) reviewed the previously named †*Phareodus* species; he recognized three valid North American species: †*Phareodus acutus* Leidy, †*Phareodus encaustus*, and †*Phareodus testis*. However, his morphological description was mainly based on the very few specimens referred to †*Phareodus acutus* Leidy (1873), which is a junior

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*A version of the second part of the discussion of this chapter is in press: Li Guo-qing. 1994 (in press). Systematic position of the Australian fossil osteoglossid fish †*Phareodus* (†*Phareoides*) *queenslandicus* Hills. Memoirs of the Queensland Museum, Australia.

synonym of †*Phareodus encaustus* (Cope); his statistical data on meristics were also notcomplete; and his restorations for the naso-ethmoid region, the infraorbital region, and the caudal skeleton are in need of revision.

Hills (1934) named an Australian species †*Phareodus queenslandicus* on the basis of materials from the Redbank Plains Formation of southern Queensland, Australia. It was considered to be similar either to the North American †*Phareodus acutus* [=†*Phareodus encaustus* (Cope) 1872, Grande 1984] in body shape and in the skull roof, or to the Recent Australian *Scleropages leichardti* Günther 1864 in the shape of the "post orbitals." Hills (1958) later believed that †*P. queenslandicus* might be a member of the genus *Scleropages*. Roellig (1967) agreed with Hills after examining both fossil and Recent osteoglossids. In contrast, Taverne (1973, 1974, 1978) asserted that †*P. queenslandicus* differed as much from the North American †*Phareodus* species as it did from †*Brychaetus* (Woodward, 1901); he thus coined another generic name, †*Phareoides*, (see Taverne, 1973), for †*Phareodus queenslandicus.*

The most recent revision of the North American †*Phareodus* species was made by Grande in 1984, but his emphasis is on postcranial characters, particularly on meristic features. Grande's revision resulted in the recognition of only two valid species: †*Phareodus encaustus* and †*Phareodus testis.*

Since Grande published the first edition of his monograph on the Green River fossil fauna in 1978 (see Grande, 1984), many new specimens of †*Phareodus* have been collected from the Green River Formation (e.g., Fig. 2-1). Recently, FMNH and AMNH offered me an opportunity to examine all of the new materials of †*Phareodus* deposited in their collections. In addition, Queensland Museum lent me casts and original specimens referred to †*Phareoides queenslandicus.* My examination of these materials suggests that the validity of †*Phareodus* species need to be revised.

This chapter will focus on the following goals: (1) giving a detailed description of †*Phareodus* species based on the specimens recently collected from the Green River Formation, (2) clarifying the valid North American †*Phareodus* species, and (3) assessing the validity of the genus †*Phareoides* Taverne.

Comparative Materials

Specimens studied for this chapter consist of fossil specimens, Recent dried skeletons, and preserved Recent specimens.

Hiodontiformes– Hiodontidae: *Hiodon tergisus* Lesueur, specimens listed in Chapter 6. *Hiodon alosoides* (Rafinesque), specimens listed in Chapter 6. †*Hiodon*

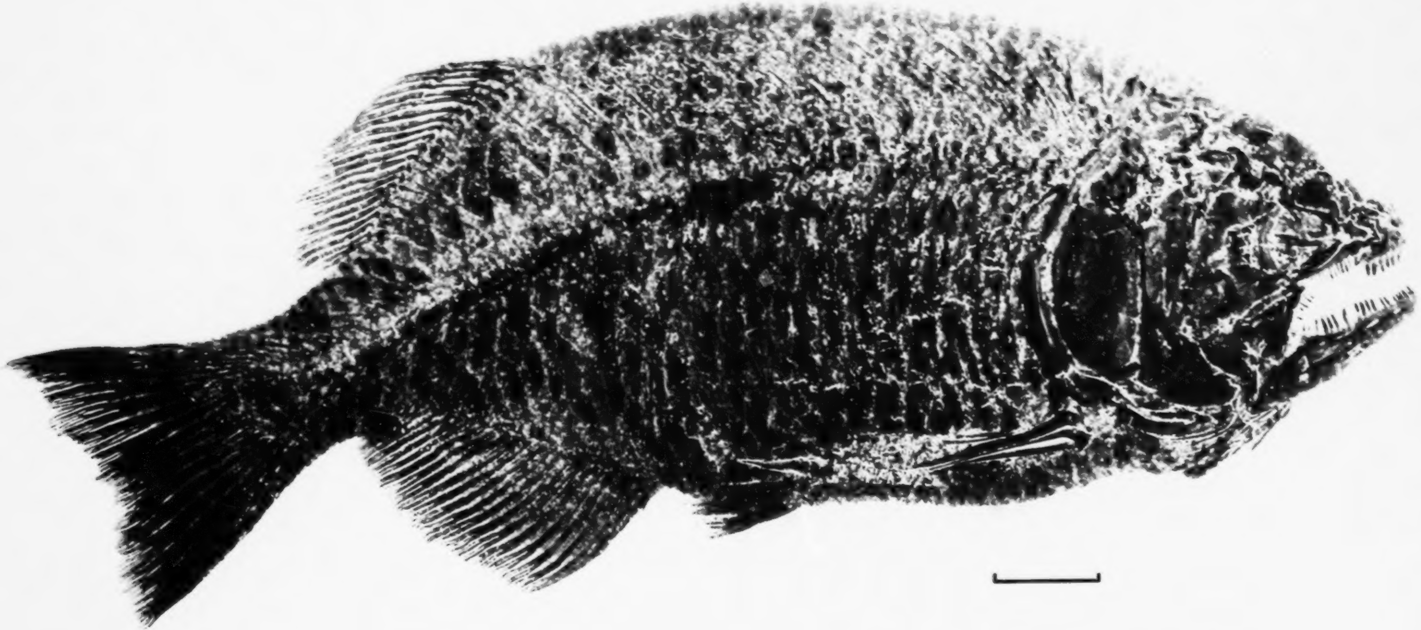

FIGURE 2-1: FMNH PF14040, one of the new specimens of †*Phareodus encaustus* from the F-1 of Tinsky 1988 Quarry, Lincoln County of Wyoming. Scale bar equals 46mm.

consteniorum, specimens listed in Chapter 6. †*Eohiodon rosei* (Hussakof), UALVP 12436 and specimens listed in Cavender (1966). †*Eohiodon woodruffi* Wilson, specimens listed in Wilson (1978) and Chapter 5. †*Eohiodon falcatus* Grande, specimens listed in Grande (1979) and Chapter 5. †*Yanbiania wangqingica* Li, specimens listed in Li (1987).

Osteoglossiformes– Osteoglossidae: *Osteoglossum bicirrosum* (Vandelli), one alizarin prepared specimen (UAMZ 4642, SL = 177). *Osteoglossum ferreirai* Kanazawa, four alizarin prepared young specimens (UAMZ 6753-6754, SL ranging from 48 to 61). †*Phareodus queenslandicus* Hills, casts of specimens listed in Hills (1934); *Arapaima gigas* (Cuvier), one specimen (UAMZ 2244, SL=285). †*Sinoglossus lushanensis* Su, specimens listed in Su (1986).

Pantodontidae: *Pantodon buchholsi* Peters, one alizarin prepared specimen (UAMZ 6751, SL=72; three specimens preserved in alcohol (UAMZ 2273, SL ranging from 60 to 67).

Notopteridae: *Notopterus chitali* (Hamilton), four alizarin prepared specimens (UAMZ 6756, SL ranging from 72 to 82). *Xenomystus nigri* (Günther), two complete alizarin prepared specimens (UAMZ 2272, SL=132; UAMZ 6752, SL=125).

SYSTEMATIC PALEONTOLOGY

Subdivision Teleostei Müller, 1846
Superorder Osteoglossomorpha Greenwood et al., 1966
Order Osteoglossiformes Berg, 1940
Suborder Osteoglossoidei Berg, 1940
Family Osteoglossidae Bonaparte, 1850
Subfamily Osteoglossinae Bonaparte, 1850

Included Genera– †*Cretophareodus gen.* nov., †*Phareodus*, *Pantodon*, †*Singida*, *Osteoglossum*, and *Scleropages*.

Emended Diagnosis– Osteoglossids differing from Heterotidinae in the following features: basihyal tooth plate fused with basibranchial tooth plate; jaw articulation behind vertical middle line of orbit; horizontal arm of preopercle short, ending anteriorly far behind orbit; preoperculo-mandibular canal opening in a groove on horizontal arm of preopercle; opercle subsemicircular; presence of fused palato-ectopterygoid; first pectoral fin ray particularly strong and long, with distal end extending to or beyond pelvic fin.

Remarks– †*Cretophareodus* is a new member of the Osteoglossinae named on the only specimen from the Upper Cretaceous Oldman Formation of southeastern Alberta. A detailed description and discussion of †*Cretophareodus* is given in Chapter 3.

†*Brychaetus* (Woodward, 1901) was supposed to be osteologically similar to both †*Phareodus* (Leidy, 1873) and †*Phareoides* (Taverne, 1973). A comparison of the observable cranial skeleton of †*Phareodus encaustus* with that of †*Phareoides queenslandicus* and †*Brychaetus muelleri* (Roellig, 1974) suggests possible synonymy of both †*Phareoides* and †*Brychaetus* with †*Phareodus* (see the discussion for details).

†*Singida* (Greenwood and Patterson, 1967) is tentatively included in the subfamily Osteoglossinae because it shares at least five of the seven emended diagnostics of the subfamily (opercle subsemicircular, short horizontal arm of preopercle ending anteriorly far behind the orbit, preoperculo-mandibular canal opening in a groove on horizontal arm of the preopercle, jaw articulation far behind the orbit, and the particularly strong and long first pectoral fin ray). In addition, this African fossil genus also shares another four synapomorphies with the extant *Osteoglossum* and *Scleropages*: 1) postero-ventral edge of the opercle distinctly concave, 2) nasals meeting each other, 3) strongly upturned mouth cleft (see Greenwood and Patterson, 1967), and 4) hypurals reduced to five. These shared character states indicate that †*Singida* is more closely related to *Osteoglossum* and *Scleropages* than it is to other genera in Osteoglossomorpha.

Pantodon has always been considered to be a specialized lineage of Osteoglossoidei. My study suggests that it is most closely related to the extant *Osteoglossum* and *Scleropages*. This relationship is strongly supported by the character states in the emended diagnosis of Osteoglossinae as well as by the strongly upturned mouth cleft and some features from the anatomy of the pectoral girdle (see Greenwood and Thomson, 1960).

Genus †*Phareodus* Leidy, 1873

-*Osteoglossum* Cope, 1872: 429
-*Phareodus* Leidy, 1873: 99
-*Phareodon* Leidy -Cope, 1873: 637
-*Dapedoglossus* Cope, 1877a: 807

-*Dapedoglossus* Cope -Cope, 1877b: 570
-*Dapedoglossus* Cope -Cope, 1883: 68
-*Phareodus* Leidy -Thorpe, 1938: 287
-*Phareodus* Leidy -Roellig, 1967: 137
-*Phareoides* Taverne, 1973: 497-499
-*Phareodus* Leidy -Taverne, 1978: 7
-*Phareodus* Leidy -Grande, 1984: 69

Type species– †*Phareodus encaustus* (Cope)

Emended Diagnosis– Osteoglossinae differing from other genera in having following features: anterior part of frontal at least 1.5 times as broad as posterior part, extrascapular angular, depth to width of opercle ratio 2-2.5, teeth on premaxilla ranging from 7 to 9 (never more than 9), first ural bearing two complete neural spines, TV 47-51, PFR 7-10, DFR 16-21, DP 18-24, AFR 22-28, AP 22-28, H 5-6, CFR i-8-7-i.

†*Phareodus encaustus* (Cope), 1870

(Figs. 2-1 - 2-5, 2-6A, 2-11B, 2-12B-C, and 2-13B)

-*Osteoglossum encaustum* Cope, 1872: 430
-*Phareodus acutus* Leidy, 1873: 99
-*Phareodon acutus* Leidy -Cope, 1873: 637
-*Phareodon sericeus* Cope, 1873: 638
-*Dapedoglossus encaustus* Cope, 1877a: 808
-*Dapedoglossus aequipinnis* Cope, 1878: 77
-*Dapedoglossus encaustus* Cope, 1883: 70
-*Dapedoglossus acutus* (Leidy) -Cope, 1883: 72
-*Dapedoglossus aequipinnis* Cope -Cope, 1883: 73
-*Phareodus encaustus* (Cope) -Thorpe, 1938: 287
-*Phareodus aequipinnis* (Cope) -Thorpe, 1938: 287
-*Phareodus brevicaudatus* Thorpe, 1938: 289-290
-*Phareodus acutus* Leidy -Roellig, 1967: 138-141
-*Phareodus encaustus* (Cope) -Roellig, 1967: 143
-*Phareodus encaustus* (Cope) -Grande, 1984: 71-73

Holotype– AMNH 2793, part of the right side of the abdominal region with series of scales.

Referred Specimens– Complete: FMNH PF10256, 10285, 10964, 10965, 10966, 10967, 11944, 11945, 12408, 12681, 14040, and 14063. SL ranges from 26-540mm (see Appendix 2-I for details). Incomplete: FMNH PF9891, 10255, 10257, 10961, 10962, 10963, 11938, 11952, 12515, 12683, 12685, 13103, 14064, 14262; AMNH 2472, 4587, 8999, and 19441.

Type Locality– Fish slate cut on the Green River (Cope, 1872: on the line of the Union Pacific Railroad), Kemmerer, Lincoln County, Wyoming, USA.

Horizon– Fossil Butte Member, Green River Formation, late early Eocene.

Emended Diagnosis– Frontal at least twice as broad anteriorly as posteriorly, hyomandibular bearing a long stick-like opercular process and a subtriangular anterior wing, upper posterior infraorbital longer than deep, at least twice as deep as lower one, TV 49-51 (22-25 PCV + 25-27 CV), BR 9-10, VFR 4-6, DFR 17-22 (mainly 18-21), DP 18-24 (mainly 18-21), AFR, 22-25, AP 25.

Description

Remarks on Holotype– †*Phareodus encaustus* (Cope) was initially named only on the holotype, which is a portion of the right side of a large individual, showing only several series of the flank scales. Cope (1872, 1883) gave a rather detailed description of the holotype but no diagnosis for the species. Since then a number of completely preserved specimens collected from the Green River Formation have been added to this species. Although Roellig (1967) and Taverne (1977, 1978) made a detailed revision of this North American fossil osteoglossid, no comprehensive description has been given of the type species. Grande (1984) believed that Leidy's (1873) †*Phareodus acutus* is a synonym of †*Phareodus encaustus* (Cope). In addition, he also suggested that †*Phareodus sericeus* Cope (1873), †*Dapedoglossus aequipinnis* Cope (1878), and †*Phareodus brevicaudatus* Thorpe (1938) are all synonymous with †*Phareodus encaustus*. My examination of the new materials of †*Phareodus* from the Green River Formation (most of them are well preserved) confirms Grande's assessment. The following description is based on all of the referred specimens listed in this chapter.

Body Shape and Size– The body of this fish is elongate and fusiform in the juvenile, and deeper or oval in the adult (see Fig. 2-1). It is dorsally much more distinctly arched than ventrally, with the dorsal edge gradually inclined posteriorly to a point before the pelvic fin. The body size of the adult may reach or exceed 540mm in standard length (Appendix 2-I).

Skull Roof– This fish has a relatively smooth skull roof as shown on the dorsal view of FMNH PF10256, 11946, 12681, 12683, 14040, 14262, and on AMNH 4587, 8999. All of the bones forming the skull roof are well preserved on most of the specimens (e.g. Fig. 2-2A).

The nasal is curved, in the shape of the lower end of a hockey stick with the anterior 1/3 downturned to articulate with the strongly developed ascending process of the premaxilla (Fig. 2-5A). The posterior portion of this bone overlaps the antero-medial margin of the frontal (e.g., FMNH PF10256 and 14040) (Fig. 2-3). Between the two nasals is the rhomboid mesethmoid that completely separates the left nasal from the right.

Posterior to the nasal and the mesethmoid are the frontals, the largest bones on the skull roof. Each frontal is greatly expanded anterolaterally to form an anterior portion at least twice as broad as the posterior portion of this bone. The suture between the two frontals is slightly interdigitated (e.g., FMNH PF10256 and 12683). On the laterally expanded anterior portion of the frontal there may be one to two crests parallel to the suture between the two frontals. On those frontals from which the nasal has been disarticulated, the nasal leaves a distinct arched depression on the antero-medial margin of each of the frontals (e.g., FMNH PF12683, 10256, and AMNH 4587 and 8999).

Posterior to and interdigitating with the frontal is the somewhat trapezoidal parietal. This bone bears a slightly anteriorly curved trans-occipital crest on its occipital margin. Immediately behind this crest, the parietal suddenly sinks to form a distinct wide depression (also called the "fosse occipito-dorsale," see Taverne, 1973 and 1978) with the lateral part of the supraoccipital and the epiotic. The suture between the two parietals is also slightly interdigitated.

The supraoccipital is dorsally crested. As in the other species of Osteoglossinae, this bone does not anteriorly separate the left parietal from the right (e.g, FMNH PF 14262 and AMNH 4587). Postero-ventral to the supraoccipital lie the two irregularly shaped exoccipitals.

The epiotic is postero-laterally sutured to the supraoccipital and the parietal. It is irregularly triangular with a strong postero-lateral process. This bone forms the posterior wall of the neurocranium with the parietal and the supraoccipital.

The extrascapular is tubular and "V"-shaped with the lateral arm broader than the mesial arm. It is dorsal to the epiotic and the supraoccipital, and posteriorly connects with the posttemporal (e.g., FMNH PF12681) (Fig. 2-2A).

The dermopterotic is elongate with a triangular postero-lateral corner. Both the

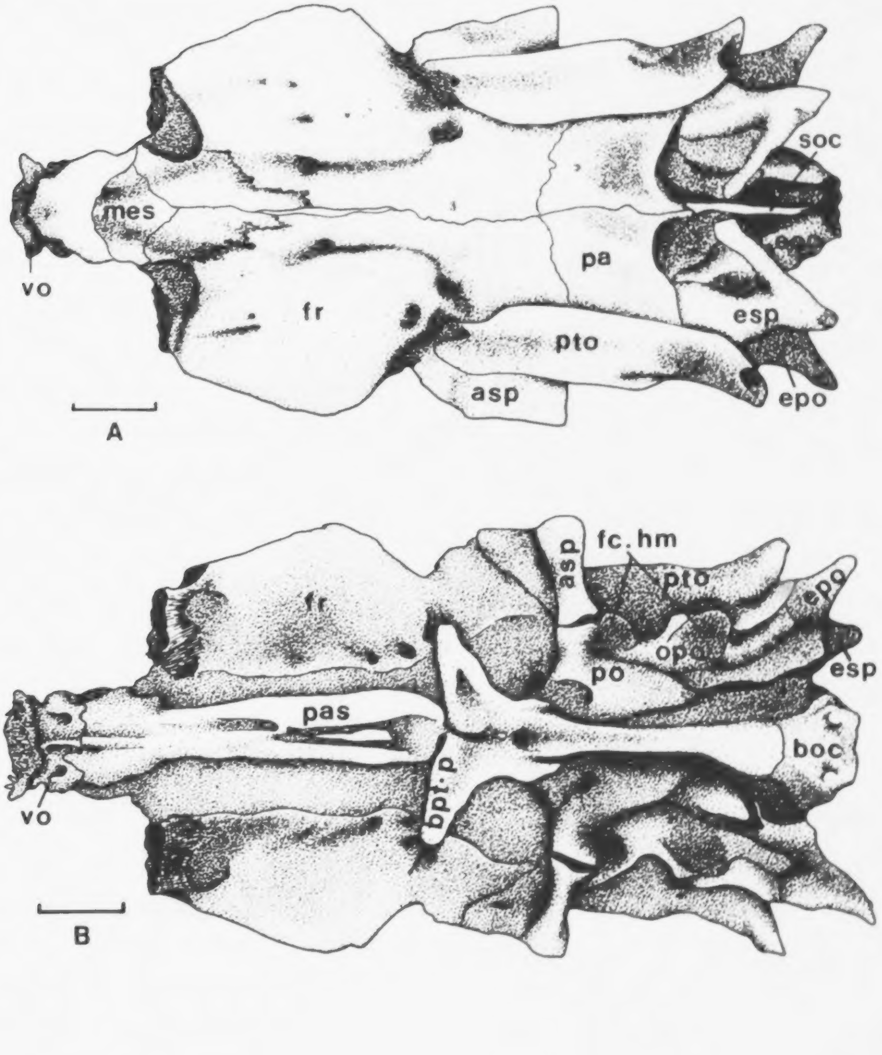
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FIGURE 2-2: †*Phareodus encaustus*, showing the basic structure of the dorsal (**A**) and ventral (**B**) views of the neurocranium, based on AMNH 4587. Scale bars equal 10mm.

anterior portion, which overlaps the autosphenotic, and the posterior portion of this bone are slightly narrower than its medial portion. From posteriorly to anteriorly it is mesially sutured with the epiotic, the parietal, and the frontal. The postorbital canal of the lateral line system enters the dermopterotic from the postero-lateral corner of this bone.

The autosphenotic has a strong posterior ridge on its ventral side, which sutures with the ridged part of the prootic.

On the ventral suface of the pterotic and the prootic is developed an articulation facet for the head of the hyomandibular. This indicates that the relationship between the hyoid arch and the neurocranium in this fish is slightly different from that in the Recent osteoglossids, in which the articulation facet for the hyomandibular is confined within the pterotic (Kershaw, 1976).

Floor of Neurocranium– As in the Recent *Osteoglossum* and *Scleropages*, the floor of the neurocranium of this fish is mainly formed by the basioccipital, the parasphenoid, and the single vomer (e.g., FMNH PF10255, 12685, 14262, and AMNH 4587) (see Fig. 2-2B).

The basioccipital is thicker posteriorly than anteriorly with two small postero-ventral processes.

The parasphenoid (Fig. 2-2B) is a sword-like bone that extends almost all the way along the skull floor, bearing a pair of strong basipterygoid processes articulating with the postero-dorsal end of the endopterygoid. Teeth are almost absent from the ventral side of this bone, there being only one to three conical ones between the two basipterygoid processes.

The vomer is more or less shovel-shaped in ventral view, with conical teeth (about 20 in number) of moderate size on its antero-ventral side (AMNH 4587). It appears to have fused with the anterior end of the parasphenoid.

Opercular Series– The opercular region (Fig. 2-3) is well preserved on FMNH PF 14040, 12681, 11944, 12525, 12683, and AMNH 4587. The preopercle (e.g., Fig. 2-5D) is slightly curved, with an indistinct horizontal arm that extends anteriorly only to the level of the postero-ventral corner of the 3rd infraorbital (the shallow lower posterior infraorbital). It is surficially strongly ridged; however, the disarticulated left preopercle on FMNH PF11946 and 12681 suggests that the internal surface (mesial view) of this bone is rather smooth. The vertical arm is nearly as broad as the horizontal arm. As in the Recent Osteglossinae, the preoperculo-mandibular canal on the horizontal arm of this bone opens in a groove.

As in the Recent *Osteoglossum* and *Scleropages*, the opercle in this fish is large and semicircular in outline with a relatively straight anterior edge and a rounded posterior edge. Except the dorsal 1/7 and the anterior margin overlapped by the preopercle, all of the area of the external surface of this bone is radially sculptured, with each of the radii consisting of numerous fine granular swellings. Measurement of 17 complete opercles (Table 2-1) suggests that this bone has a depth to width ratio 2-2.5 (average 2.12). The postero-ventral edge of the opercle in this fish is not concave, unlike that in the Recent *Osteoglossum*, *Scleropages*, and in the fossil †*Singida*.

Both the subopercle and the interopercle are triangular or crescentic in shape.

Orbital Region– This region is completely preserved on FMNH PF 12681 and 14040 (Fig. 2-3). The antorbital is somewhat branched with its postero-ventral end joining with the anterior end of the first infraorbital.

The first infraorbital is slender with its posterior part slightly deeper than its anterior part. The second infraorbital is small but deeper than the first infraorbital. These two form the ventro-lateral wall of the orbit.

The two posterior infraorbitals (infraorbitals 3 and 4-5) are large and broad with their external surface radially sculptured. Unlike those in †*Phareodus testis*, the lower one (io3) is much shallower than the upper one (io4-5) although it is more expanded posteriorly than anteriorly with a reduced anterior portion and a convex dorsal edge. The upper one is the largest, nearly twice as deep as the lower one, and more or less fan-shaped. Previously this largest upper posterior infraorbital in the Osteoglossomorpha was considered to be the fused infraorbital 3 plus infraorbital 4 (e.g., Nelson, 1969b; Greenwood, 1970; Taverne, 1977, 1978; Kershaw, 1976). A comparison of these two large posterior infraorbitals with the primitive condition in †*Leptolepis*, †*Allothrissops*, and the Recent *Elops* (Patterson, 1967; Goody, 1969; Forey, 1973a-b; Nybelin, 1974; Patterson and Rosen, 1977) indicates that the largest, upper posterior infraorbital in the Osteoglossomorpha has resulted from fusion of io4 with io5 rather than io3 with io4. This adjustment is confirmed by the situation in the Late Jurassic to Early Cretaceous †*Lycoptera* and the Aptian †*Laeliichthys*, in which io4 and io5 are present as independent elements.

The demosphenotic is a somewhat triangular and tubular bone (e.g., FMNH PF12683 and 14040). It is dorsal to the anterior part of the largest upper posterior infraorbital and posteriorly overlaps the autosphenotic.

The dorso-medial wall of the orbit is formed by three cartilaginous bones: the orbitosphenoid that is ventral to the laterally expanded anterior portion of the frontal, the basisphenoid that is ventro-medial to the orbitosphenoid, and the pterosphenoid that

TABLE 2-1: Ratio of depth to width of opercle of †*Phareodus encaustus*.

SPECIMENS	OPD	OPW	OPD/OPW
AMNH 4587	85	38	2.24
FMNH PF10256	91	42	2.17
FMNH PF10961	9	4.5	2.00
FMNH PF10963	7	3.5	2.00
FMNH PF10964	10	4	2.50
FMNH PF10965	6	3	2.00
FMNH PF10966	5	2.5	2.00
FMNH PF10967	12	6	2.00
FMNH PF11944	91	42	2.17
FMNH PF11945	90	40	2.25
FMNH PF12408	7	3.5	2.00
FMNH PF 12515	90	39	2.31
AMNH PF12681	92	40	2.30
FMNH PF12683	91	40	2.28
FMNH PF12685	96	43	2.23
FMNH PF14040	98	42	2.33
FMNH PF14062	22	11	2.00
AVERAGE			2.12

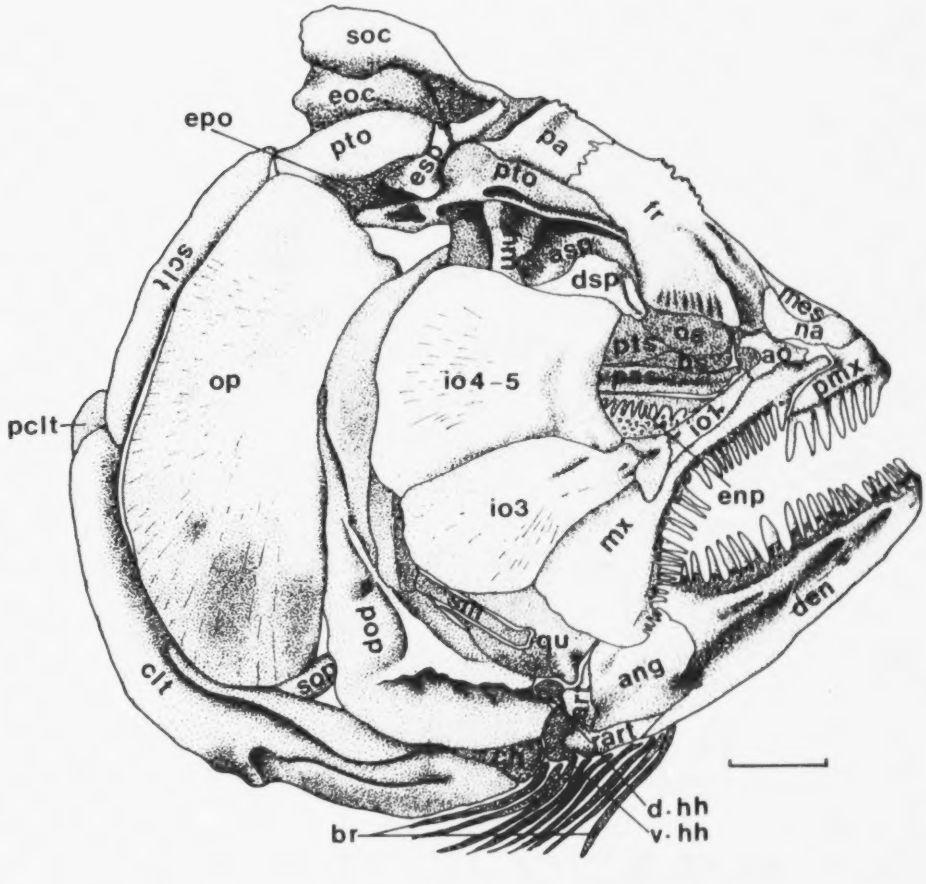
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FIGURE 2-3: †*Phareodus encaustus*. Line drawing of the skull of FMNH PF14040, showing the preserved structures described in the text. Scale bar equals 20mm.

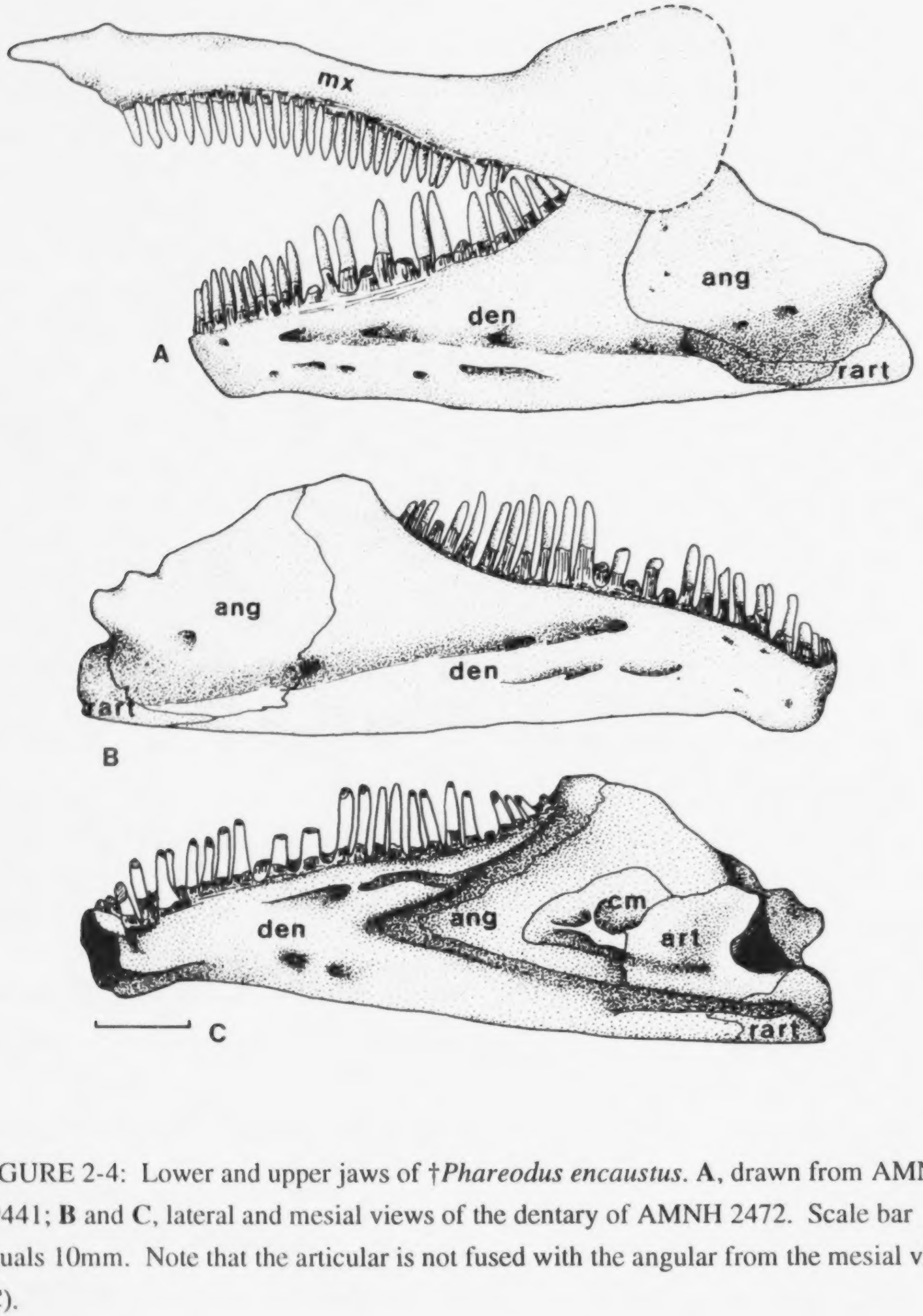
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FIGURE 2-4: Lower and upper jaws of †*Phareodus encaustus*. **A**, drawn from AMNH 19441; **B** and **C**, lateral and mesial views of the dentary of AMNH 2472. Scale bar equals 10mm. Note that the articular is not fused with the angular from the mesial view (**C**).

inserts anteriorly between the orbitosphenoid and basisphenoid.

The supraorbital is absent in this fish.

Jaws– The upper and lower jaws appear to be intermediate between those in the Recent Osteoglossinae and Heterotidinae. The premaxilla is unique in Osteoglossidae in having an outline resembling a runner's spiked shoe (e.g. Fig. 2-5A). At the top of the raised anterior part of this bone develops a distinct articulation facet to receive the downturned anterior end of the nasal (FMNH PF10256, 10283, 12515, 12638, and 14040). The strongly tapering posterior part is overlapped by the anterior end of the maxilla. Teeth on this bone are conical and the largest among the teeth in the jaws, numbering from seven but never more than nine.

The maxilla on FMNH PF12683, 11944, 14040, 10256, 10285, 11946, 12515, 12681, and AMNH 19441 is slightly dorsally curved with a deep posterior portion, which is shovel-shaped, and a more or less tapering anterior extremity overlapping the posterior part of the premaxilla (e.g. Figs. 2-4A and 2-12B). A distinct dorsal swelling is developed on the anterior portion of this bone at the level behind the premaxilla. A complete maxillary dentition on FMNH PF10256 consists of at least 34 conical teeth that are gradually smaller posteriorly. The posterior end of the maxilla extends posteriorly to near the level of the quadrate condyle.

A supramaxilla is absent in this fish.

The dentary (e.g., FMNH PF14040, 12515, 11946, 11944, 19441, and AMNH 2472) is raised posteriorly to form a moderate coronoid process. Its posterior edge is moderately curved anteriorly. Externally it is perforated by three to four branches of the preoperculo-mandibular canal (Fig. 2-4A-B) and roughly sculptured. Mesially it bears a large, triangular posterior depression to receive the sharp triangular anterior part of the angular (Fig. 2-4 C). A complete dentary tooth set consists of at least 25 large conical teeth.

The angular is irregularly triangular with a sharp anterior portion inserting in a mesial groove in the dentary. Mesial to the angular are the endochondral corono-meckelian, which is small and irregular in shape, and the articular, which is much thicker posteriorly than anteriorly. As shown by FMNH PF14040 and AMNH 2472, the angular is definitely not fused with the articular in this fish (Fig. 2-4C).

FMNH PF14040 and AMNH 2472 also indicate that the articulation facet for the quadrate in the lower jaw is confine to the postero-dorsal surface of the articular, confirming the description given by Nelson (1973) (Fig. 2-4C).

Postero-ventral to the angular and articular inserts the small claw-shaped retroarticular.

Palato-quadrate Arch– As in the Recent *Osteoglossum* and *Scleropages*, the palatine (possibly the dermal portion) is fused with the ectopterygoid to form a palato-ectopterygoid (=ectopterygoid-palatine, Hills, 1934; Roellig, 1967; Kershaw, 1976; Taverne, 1977, 1978), with teeth mainly on the ectopterygoid part (e.g., FMNH PF10256 and 12683). The posterior edge of this fused bone is interrupted by a notch (Fig. 2-5-B).

A complete right endopterygoid is shown on FMNH PF10255. This bone is triangular with a row of large teeth along the dorso-mesial margin and small teeth on the remainder. The endopterygoid is almost identical with that in the Recent *Osteoglossum* and *Scleropages*. The only differences are (1) the anterior end of the endopterygoid is not antero-dorsally directed, and (2) the endopterygoid does not have a stick-like postero-ventral extension, whereas in *Osteoglossum* and *Scleropages* it has, shaped in lateral view like the holster of a pistol.

The metapterygoid is covered by the posterior infraorbitals on most specimens. FMNH PF12683 shows two disarticulated metapterygoids between the displaced skull roof and the two posterior infraorbitals. They appear similar to the metapterygoid in the Recent *Osteoglossum* and *Scleropages* in shape and in having no teeth.

The quadrate (FMNH PF12681, 11946, and 11947) and the symplectic resemble the corresponding bones in the Recent *Scleropages* in general outline (Fig. 2-5C). The quadrate has a "peg-like" (Kershaw, 1976) head articulating with the articular in the lower jaw. The articulation between the quadrate and the lower jaw lies below the postero-ventral corner of the 3rd infraorbital.

Hyoid Arch– Not all elements of this arch are exposed on most of the referred specimens. The left hyomandibular on FMNH PF10255 (internal view) and FMNH PF10285 (external view) indicates that this bone has only a single large head articulating with the neurocranium in a facet lying on the pterotic and the prootic. Unlike that in Recent osteoglossids, the hyomandibular in this fish bears a long, stick-like opercular process joining the opercle. In addition, it has also an expanded triangular anterior wing extending anteriorly to the level of the posterior edge of the orbit. The internal surface of the hyomandibular is rather smooth, but the external (lateral) view shows a strong vertical ridge on the posterior part of this bone. The vertical ridge extends from the head articulating with the neurocranium to the ventral tip joining with the symplectic, shaped like the butt of a rifle (Fig. 2-13B)

The ceratohyal (FMNH PF10255 and 12683) is large, imperforate, and broadly concave on both the dorsal and ventral sides.

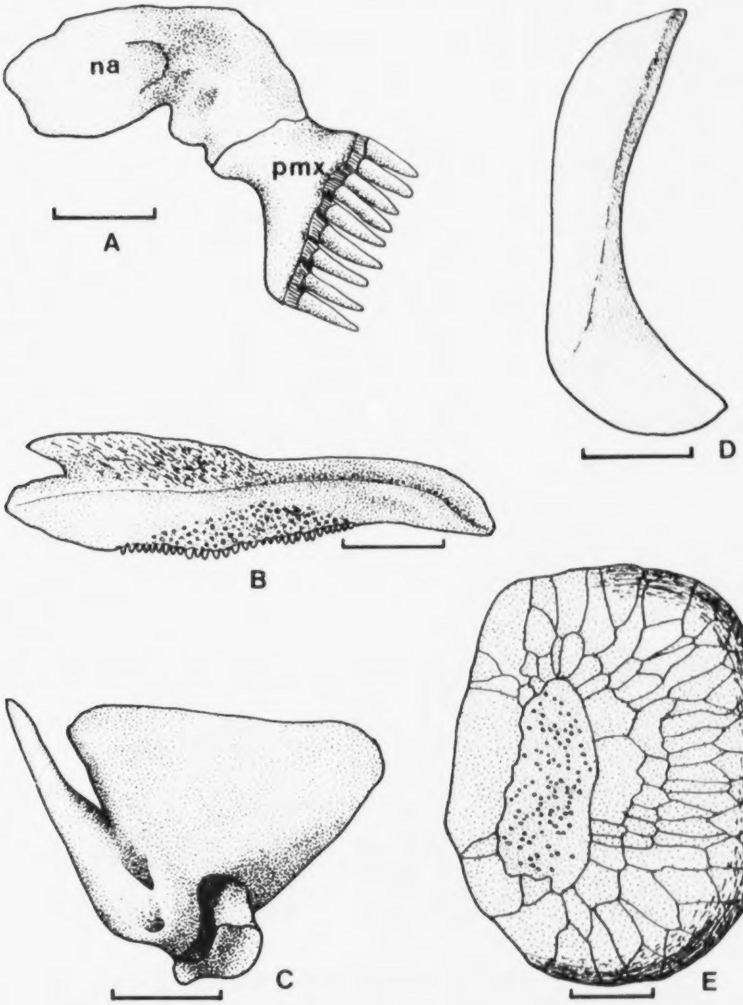

FIGURE 2-5: Some of the disarticulated bones of †*Phareodus encaustus*. **A**, nasal and premaxilla; **B**, fused palato-ectopterygoid. Both **A** and **B** are drawn from FMNH PF10256, with scale bars equal 15mm. **C**, quadrate, based on FMNH PF11946; scale bar equals 10mm. **D**, mesial view of the preopercle from FMNH PF12681; scale bar equals 20mm. **E**, trunk scale, drawing on FMNH PF12415; scale bar equals 4mm.

A disarticulated tooth plate is nearly completely exposed on FMNH PF10255 (between the two ceratohyals, partly covered by the anterior end of the hrizontal arm of the preopercle) and PF10256 (ventral to the dentary). It appears to have the same pattern as that in the Recent *Osteoglossum* and *Scleropages*, in which the basihyal tooth plate is fused with the basibranchial tooth plate. The teeth on this plate are distributed in the same way as those on the basihyal-basibranchial tooth plate in *Osteoglossum* and *Scleropages*, with the small ones on the central part and the large ones around the edges.

Nine to 10 slender branchiostegals are present in this fish (Tables 2-2 and 2-5).

Cephalic Lateral Line system– The cephalic lateral line system is distributed in the same pattern as that in the Recent *Osteoglossum* and *Scleropages*. The lateral line system from the trunk region goes into the cephalic region through the posttemporal, it enters the dermopterotic from the postero-lateral corner of the bone and then divides into two branches: one goes into the preopercle to meet the preoperculo-mandibular canal, and the other anteriorly passes through the dermopterotic to join with the infra- and supraorbital canals at the place where the frontal starts to become laterally expanded. The preoperculo-mandibular canal opens in a groove on the horizontal arm of the preopercle and then goes into the lower jaw through the retroarticular, giving out three to four branches in the dentary.

The supraorbital canal extends from the anterior end of the frontal to the nasal, ending posteriorly only in the frontal at its posterior 1/3 portion.

The infraorbital canal goes through the infraorbitals along the orbital margin of these elements. As in the Recent osteoglossids, the infraorbital canal in this fish also ends anteriorly in the antorbital (Fig. 2-3).

Pectoral Girdle and Fin– A complete pectoral girdle is preserved on FMNH PF14040 (see Fig. 2-3). The cleithrum (FMNH PF10255 and 14040) is an arched bone that consists of dorsal and ventral limbs meeting at an obtuse angle. The ventral limb is slightly broader than the dorsal limb, and laterally projecting, with its anterior end extending also to the level of the postero-ventral corner of the 3rd infraorbital. The dorsal limb is dorsally slightly tapered and about 7/8 the length of the ventral limb.

The supracleithrum is slender and both ventrally and dorsally tapered. Its dorsal half appears to be tubular to contain the lateral sensory canal, while its tapered ventral end overlaps the dorsal end of the cleithrum.

Antero-dorsal to the supraclethrum is the hook-like or "L"-shaped posttemporal (e.g., FMNH PF10255, 14040). The dorsal part of this bone is anteriorly broader than posteriorly and much longer than the ventral part. Correspondingly, the lateral line sensory canal in this bone is divided into two branches, of which the one in the ventral part extends anteriorly to enter the dermopterotic.

FMNH PF10255, 10256, 10285, and 12683 show the disarticulated coracoid. It is in the shape of the blade part of a hockey stick. There is a wide postero-dorsal concavity at the posterior 1/4 of this bone and a large oval perforation below the concavity. Dorsal to the coracoid on FMNH PF10256 is a more or less trapezoidal bone which is here identified as the mesocoracoid.

The scapula appears to be visible on FMNH PF10256. It is dislocated at the right side of the coracoid and the mesocoracoid, and also has an oval perforation.

A small scale-shaped postcleithrum is present just posterior to the joint between the cleithrum and the supracleithrum.

The pectoral fin is ventral to the obtuse angle of the cleithrum. Altogether seven to 10 pectoral fin rays are counted (Table 2-2), of which the first one is particularly strong and long, and distally segmented but unbranched, extending posteriorly to beyond the beginning of the pelvic fin, or even to reach to the beginning of the anal fin (FMNH PF12891). The others are both distally segmented and branched.

Pelvic Girdle and Fin– The pelvic girdle, which is partly exposed on FMNH PF10256, 10285, and 12685, consists of two slender tapering innominata [Men et al., 1987, synonym of pelvic fin support (Grande, 1979), pelvic bones (Wilson, 1978; Wilson and Williams, 1991)]. They are slightly longer than 1/2 the length of the longest pelvic fin ray.

The pelvic fin is small and ventrally located, containing only four to six slender, distally segmented and branched rays. The distance between the pelvic fin and the pectoral fin is at least 1.5 times that between the pelvic fin and the anal fin.

Dorsal and Anal Fins– Both dorsal and anal fins are rounded in outline and posteriorly located (see Fig. 2-1). My study suggests that the relative positions of the dorsal fin and the anal fin are externally variable from the juvenile to the adult. In terms of the predorsal and preanal lengths, there is a tendency for the dorsal fin to appear to move posteriorly during the development from juvenile to adult. Appendix 2-I shows that when the individual fish has a standard length less than 100mm, the dorsal fin is oposite the anal fin. However, on the largest specimen examined in this research (FMNH PF14040), the beginning of the dorsal fin is 55mm posterior to the beginning of the anal fin.

Internally, both the first (anteriormost) dorsal pterygiophore and the first (anteriormost) anal pterygiophore are connected with the same vertebral centrum, the first caudal vertebrae (=the last preural) via its neural and the haemal spines in both the juvenile and the adult. This means that both the dorsal and anal fins begin internally from the same vertebral centrum, as they also do in †*P. testis*. Therefore, the relative position of the dorsal fin to the anal fin is taxonomically unimportant in the classification of the †*Phareodus* species.

The dorsal fin is smaller than the anal fin in having 19-21 principal rays, of which the first one to two are distally segmented but unbranched, and the others are all distally segmented and branched. The last dorsal fin ray is always double. In total, 19-22 slender, proximally tapering dorsal pterygiophores are present to support the rounded dorsal fin. These dorsal pterygiophores gradually decrease in length from the anteriormost one to the posteriormost one.

The anal fin consists of 22-25 principal rays supported by 22-26 anal pterygiophores. It has a base length about 1.1-1.3 times that of the dorsal. As in the dorsal fin, the first one to two principal anal fin rays are distally segmented but unbranched, and the last one is double. The lengths of the anal pterygiophores also decrease from the first to the last.

Vertebral Column– The vertebral column is dorsally arched above the abdominal cavity. Some 49-51 vertebral centra are counted on 19 specimens (Table 2-2), the anterior 22-25 being the precaudals (=abdominal vertebrae, Grande, 1979) (including the first two or three that are covered by the cleithrum and the opercle and bear neural spines but no ribs), and the posterior 25-26 being caudals (including the two upturned urals). Except for the second ural, all of the centra are deeper than long, amphicoelous, and perforated.

Besides neural spines, all precaudal vertebrae bear slender epineurals postero-dorsal to the neural arches. These epineurals decrease in length posteriorly. Strong parapophyses (hémapophyses, Taverne, 1977, 1978) are developed on each of the precaudals except the first two or three centra anterior to the cleithrum. The slender, slightly curved pleural ribs articulate with the centra via the parapophyses, and extend almost to the ventral wall of the abdominal cavity. Epipleurals are absent.

Except for the two urals, which bear the hypurals, and the first to fourth preurals, which carry the enlarged (lengthened) neural and haemal spines to support the caudal fin, all other caudal vertebrae have distally tapering neural and haemal spines that are shorter on more posterior centra. For those neural and haemal spines joining with the dorsal and anal fins, their tapering distal tips are respectively overlapped by the tapering proximal tips of the dorsal and anal pterygiophores. All of the haemal and neural arches on the caudal vertebrae are fused with the corresponding centra.

TABLE 2-2: Meristics of †*Phareodus encaustus* in AMNH and FMNH.

	PCV	CV	TV	BR	PFR	VFR	DFR	DP	AFR	AP	CFR	H	EP	SPN	NSU1	NSPU2	UN
AMNH 4587	24	26	50	8	9	5	19	21	25	25	17	6	1	?	2	1	0
FMNH PF10256	24	27	51	?	7	5	22	24	25	26	17	6	1	?	2	1	0
FMNH PF10257	23	26	49	10	9	5	21	21	24	24	17	5	1	26	2	1	0
FMNH PF10285	23	26	49	9	7	6	19	20	24	25	17	6	1	23	2	1	0
FMNH PF10963	?	?	?	?	9	?	?	19	?	?	17	5	1	?	2	1	0
FMNH PF10964	23	26	49	8	9	4	19	19	24	25	17	5	1	22	2	1	0
FMNH PF10965	23	27	50	10	10	5	19	19	23	24	17	5	1	23	2	1	0
FMNH PF10966	22	25	47	10	7	5	17	18	25	26	17	5	?	?	?	?	?
FMNH PF10967	24	27	51	10	9	5	18	21	23	24	17	5	1	23	2	1	0
FMNH PF11938	23	26	49	10	?	4	17	18	25	26	17	5	1	21	2	1	0
FMNH PF11944	23	27	50	?	7	4	19	19	?	?	17	6	1	?	2	1	0
FMNH PF11945	24	26	50	?	10	6	20	21	24	25	17	6	1	23	2	1	0
FMNH PF11952	?	?	?	?	?	?	?	?	?	?	17	5	1	?	2	1	0
FMNH PF12408	24	26	50	10	10	5	20	21	23	22	17	5	1	24	2	1	0
FMNH PF12515	?	?	?	10	?	?	?	?	?	?	17	5	1	?	2	1	0
FMNH PF12681	24	27	51	9	7	6	19	20	25	25	17	4	1	24	2	1	0
FMNH PF12683	23	26	49	?	?	?	20	21	?	?	17	?	1	?	2	1	0
FMNH PF12685	23	26	49	?	9	4	21	21	25	26	17	6	1	?	2	1	0
FMNH PF14040	25	26	51	9	7	4	20	21	23	25	17	6	1	24	2	1	0
FMNH PF14062	23	27	50	?	7	4	18	19	23	24	17	5	1	22	2	1	0
FMNH PF14063	?	27	?	9	7	6	19	19	22	24	17	5	1	23	2	1	0
FMNH PF14064	23	26	49	?	?	5	19	22	25	25	17	?	?	22	?	1	0
AVERAGE	24	26	50	8	9	5	19	22	25	25	17	6	1	22	2	1	0

A series of slender, slightly sigmoid supraneurals is present before the first dorsal pterygiophore. The number of these elements differs from one specimen to another. On most specimens, 23-24 supraneurals are counted (e.g., FMNH PF11945, 12681, 14040, and 10967); 26 is the maximum (e.g., FMNH PF10409 and 10257). The supraneurals lie proximally between the neural spines of the precaudals, with the first immediately behind the posttemporal, and the last in front of the first dorsal pterygiophore.

Caudal Skeleton and Fin– Cavender (1966) and Greenwood (1970) restored a caudal skeleton for †*Phareodus testis*. The features shown in their illustrations mostly fit the features shown on the specimens referred to †*Phareodus encaustus* in this chapter (Fig. 2-6A). In general, the caudal skeleton appears to be intermediate between that of the Hiodontiformes and that of the Osteoglossiformes. It consists of two upturned urals and four preural centra. Ural 1 is normal in shape, and ural 2 is tapered postero-dorsaly.

There are five to six (most have five) hypurals (Table 2-2) that decrease in length and depth dorsally. Hypural 1 is the largest, with a distal end much deeper (more expanded) than the proximal end which articulates but does not fuse with the first ural centrum. Hypural 2 is slightly shorter and less deep than hypural 1. The two lower hypurals articulating with the first ural centrum support the lower lobe of the caudal fin along with the parhypural, the enlarged and lengthened haemal spine of the first preural, and three lengthened haemal spines articulating with the second to fourth preural centra. Hypurals 2 to 5 or 6 articulate with the second ural centrum. The three or four upper hypurals also are not fused with each other. A single exception may be present on FMNH PF12681, which appears to have only four hypurals in total, the uppermost one possibly representing the fused h4-5 or h4-6.

As in the Recent osteoglossids, uroneurals are absent.

Dorsal to the second ural centrum, there is one slender epural that posteriorly lies dorsal to the uppermost h5 (Fig. 2-6A) or h6 (Fig. 2-6B).

The u1 on all of the new referred specimens carries two autogenous neural arches and double complete neural spines. Both neural spines extend postero-dorsaly to articulate with the upper accessory caudal rays. A similar condition may be seen in the Recent adult *Heterotis* (e.g., Greenwood, 1966: fig. 4).

The neural spines on the first to fourth preural centra are lengthened to support the upper lobe of the caudal fin, together with the upper three or four hypurals, the single epural, and the two complete neural spines on the first ural centrum.

The caudal fin is shallowly forked with its lower lobe larger than the upper lob. A total of 17 principal caudal fin rays are counted, with the pattern of i-8-7-i (Table 2-2).

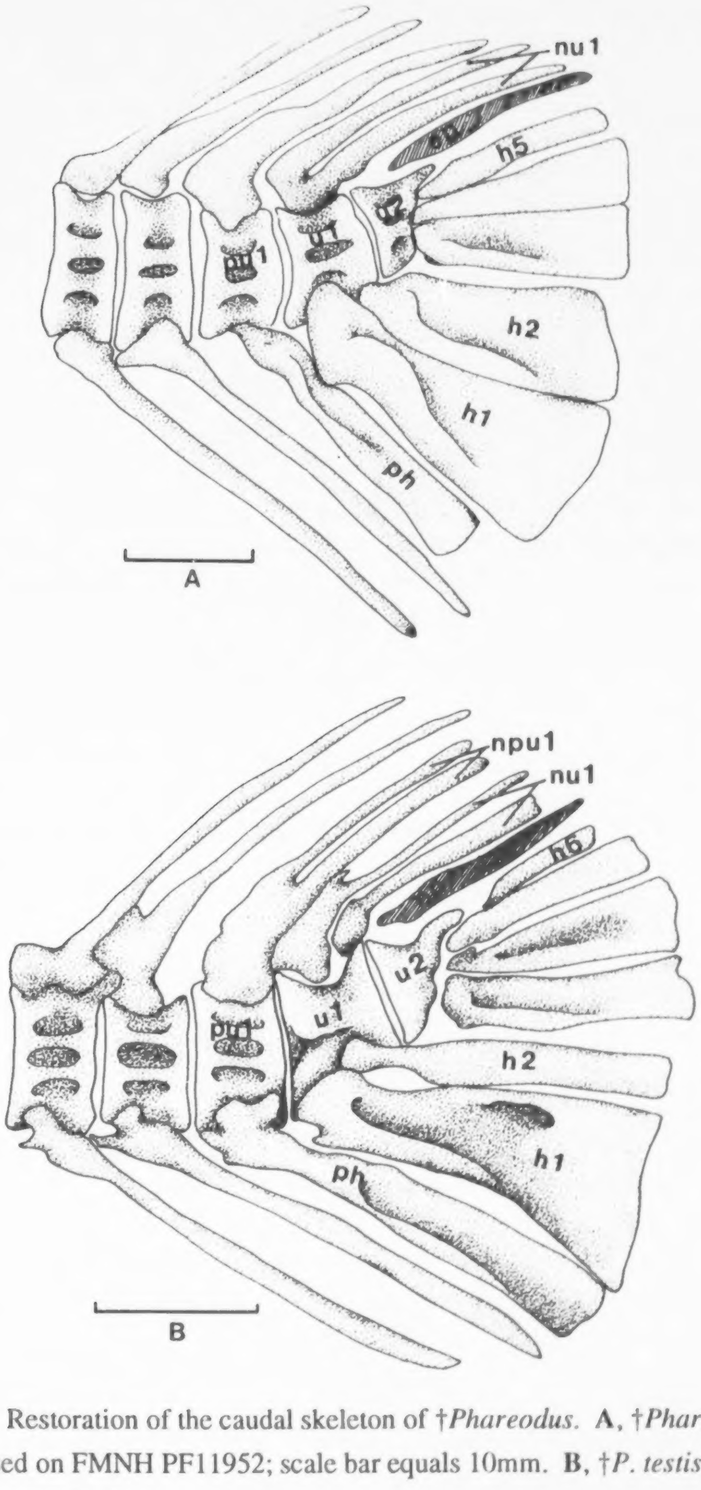
nu1
h5
u2
u1
pu1
h2
h1
ph
A
npu1
nu1
h6
u2
u1
pu1
h2
h1
ph
B

FIGURE 2-6: Restoration of the caudal skeleton of †*Phareodus*. **A**, †*Phareodus encaustus*, based on FMNH PF11952; scale bar equals 10mm. **B**, †*P. testis*, on AMNH 2799; scale bar equals 5mm.

Scales– Cope (1870, 1873) gave a detailed description of the scales covering the body of this fish. They are subcycloid and deeper than broad with no distinct latero-basal corners. The focus on each scale is granularly sculptured and basally located (subbasal nucleus). A mesial view of the scale on FMNH PF12415 shows the detail of the reticulation that is mainly developed on the apical portion posterior to the subbasal nucleus (Fig. 2-5E). The squamule units are arranged in four concentric rows on the medio-apical region and three on the dorsal and ventral region. Squamules in the most apical series are broad and largest, whereas those in the second and the third apical series are relatively smaller and narrower than those in the most apical and the most basal series. All of the other features of the scales agree with Cope's original description.

†*Phareodus testis* (Cope), 1877

(Figs. 2-6B, 2-7 to 2-9, 2-11C, 2-13C)

-*Dapedoglossus testis* Cope, 1877b: 570
-*Phareodus brevicaudatus* Thorp, 1938: YPM1418
-*Phareodus testis* (Cope, 1877) - Grande, 1984: 73-74

Holotype– USNM 4014, a nearly complete fish.

Referred New Specimens– 22 well-preserved specimens: AMNH 1336, 2799, 5821, 6301, and 11547; FMNH PF10627, 10960, 10969, 11942, 11943, 12409, 12411, 12682, 13035, 13576, 14062, 25014, and 26407; UALVP 447, 17657, 17658, and 17659. SL ranges from 39-304mm (see Appendix 2-II for details). 17 incomplete specimens: AMNH 743, 754, 805, 2467, 2471, and 8124; FMNH PF10241, 11939, 11941, 12412, 14061, and 25439; ROM 28560, 29043, and 29076; UALVP 12712; and UF 31.

Type Locality– Twin Greek, Lincoln County, Wyoming, USA.

Horizon– Fossil Butte Member, Green River Formation, late early Eocene.

Emended Diagnosis– †*Phareodus* differing from other species in having the frontal less than twice as broad anteriorly as posteriorly, hyomandibular without subtriangular anterior wing, posterior infraorbitals (io2-3 and io4-5) deeper than long, BR 9-12 (mainly 10), VFR 5-6 (mostly 6), DFR 17-20 (mostly 19), DP, 18-21 (mostly 19), AFR 25-28 (mostly 26), AP 26-28 (mostly 26).

Description

Remarks on Holotype– The holotype is well preserved, missing only part of the abdominal region and the caudal region. When Cope (1877b) named †*Phareodus testis*, he gave only a brief description of the holotype but no specific diagnosis. The two characters used by Cope to distinguish †*Phareodus testis* from †*P. encaustus* are (1) the body size and (2) the number of the teeth on the dentary. The discovery of numerous new specimens of †*P. testis* and †*P. encaustus* indicates that these two characters overlap in the two North American †*Phareodus* species; they do not descriminate †*P. testis* from †*P. encaustus* exactly.

Body Shape and Size– As in †*P. encaustus*, the body shape of this species is elongate and fusiform in juveniles and moderately deep in the adults (Fig. 2-7), with the dorsal margin posteriorly inclined to a level before the dorsal fin. The largest individul may have a total length beyond 370mm (see Appendix 2-II).

Skull Roof– In dorsal view, FMNH PF 14062 (Fig. 2-8A) and the lateral view of AMNH 2799, 11547, FMNH PF10241, 11942, 11943, 12682 (Fig. 2-8B), 13035, ROM 29043, UALVP 447, 17657, 17658, and 17659 show a smooth skull roof. The nasal is similar to that in †*P. encaustus* in the shape. A rhomboid mesethmoid that separates the left nasal from the right is also present (e.g., FMNH PF14062, 11942, and UALVP 447).

The frontal is similar to that in †*P. encaustus* in both shape and proportion. It is true that, on some specimens (e.g. UALVP 447, 17657), the broadest part of the anterior portion of the frontal is less than 1.5 times the width of the posterior portion. Most of the specimens show a frontal that has a greatly laterally expanded anterior part at least 1.5 times as broad as the posterior part (see Figs. 2-8B and 2-9). The suture between the two frontals is straight anteriorly and posteriorly but interdigitated medially, usually with two interdigitations at about 1/2 the length of the frontal (FMNH PF14062). The supraorbital canal medially passes through the anterior portion, with no branch ending in the posterior portion of this bone.

The parietal is short with a length approximately 1/5 the length of the frontal; in †*P. encaustus*, the parietal is nearly 1/3.5 the length of the frontal. The width of the parietal is as broad as that of the posterior end of the frontal. The suture between the parietal and the frontal is more or less curved (e.g., FMNH PF14062 and UALVP 12712), while the suture between the two parietals may deviate from the mid-dorsal line to the left (e.g., FMNH PF14062) or to right (e.g., UALVP 12712). Posteriorly, the parietal is similar to that in †P. *encaustus*, bearing a slightly anteriorly curved trans-occipital crest on its dorso-occipital margin. Immediately behind the crest, the parietal forms a distinct depression together with the supraoccipital and the epiotic.

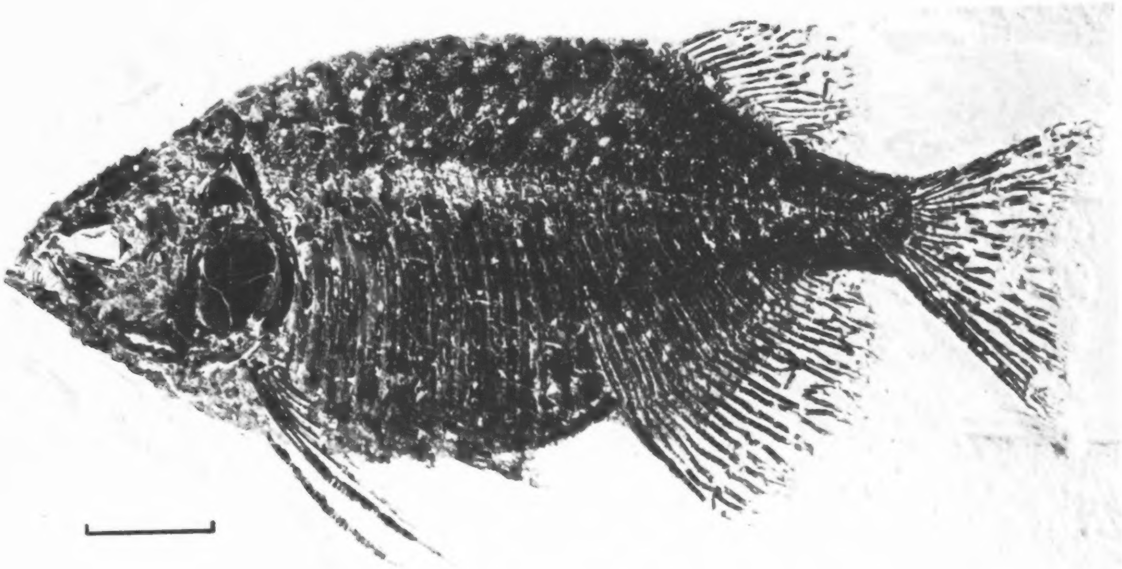

FIGURE 2-7: FMNH PF12411, one of the new specimens of †*Phareodus testis* from the F-2 of Tynsky 1986 Quarry, Lincoln County of Wyoming. Scale bar equals 20mm.

The supraoccipital (e.g., UALVP 12712) is the same as that in †*P. encaustus* in both shape and the connection to the parietals, as also is the epiotic.

The dermopterotic is braoder posteriorly than anteriorly and has a strong triangular postero-lateral process (e.g., FMNH PF11943, 12682, ROM 29043, UALVP 12712, 17657, 17658, and 17659), from which the lateral line system enters the cephalic region.

The extrascapular is identical with that in †*P. encaustus* (FMNH PF11943, 12682, ROM 29043, UALVP 17657, 17658).

The autosphenotic is partly seen on ROM 29043, and UALVP17658. It appears to be similar to that in †*P. encaustus*.

Floor of Neurocranium– Since the elements forming the floor of the neurocranium are not completely exposed, it is difficult to give a detailed description of this part.

The parasphenoid is partly seen on most of the specimens. As in †*P. encaustus*, this bone also does not bear teeth on its anterior ventral surface where it crosses the orbit.

It is noticeable that a false appearance suggesting that the parasphenoid in this species seems to bear teeth on its orbital part is seen on UALVP 17657 and 17658. A microscopic view of those two specimens shows that those teeth beneath the orbital part of the parasphenoid are the large teeth distributed along the dorso-medial margin of the endopterygoid.

The vomer shown on UALVP 447 is basically similar to that in †*P. encaustus*. It seems also to be fused with the anterior end of the parasphenoid.

Opercular Series– Besides the holotype, a complete opercular system is preserved on most of the referred new specimens, and is particularly well preserved on FMNH PF12682 (Fig. 2-8B), PF11943, 13035, ROM 29043, and UALVP 447, 12712, 17659.

Unlike that in †*P. encaustus*, the preopercle has a distinct horizontal arm about 3/5 the length of the vertical arm and meeting with the latter at an angle of approximately 90°, where the bone is the widest (Figs. 2-8 and 2-9). Both the vertical and horizontal arms are tapered dorsally and anteriorly respectively. In other respects this bones is identical with that of †*P. encaustus*.

The opercle is almost the same as that of †*P. encaustus* in both shape and proportion. Measurements of the opercle on 26 specimens (Table 2-3) suggest that its depth to width ratio is 2-2.4, also with an average of 2.12 as in †*P. encaustus*.

The subopercle and interopercle are well preserved on FMNH PF 12409 and 12682; the former is somewhat elongate and the latter triangular.

Orbital Region– The orbital region is well preserved on FMNH PF12682, ROM 29043, and UALVP 447 and 17658. Four infraorbitals including the dermosphenotic are present. The io1 is elongate and posteriorly slightly deeper than anteriorly. The io2 appears to have been fused with io3, forming the second largest (lower) posterior infraorbital that is somewhat trapezoidal and often slightly deeper than long. The fused io4-5 is much deeper than long, usually with a depth nearly 1.5 times that of the fused io2-3. In comparison with that in †*P. encaustus,* the two large posterior infraorbitals are much shorter than the two large posterior infraorbitals in †*P. encaustus*, forming a relatively short cheek region (e.g., Figs. 2-8B, 2-9, and 2-11C).

No complete dermosphenotic is seen on the specimens. It seems to be similar to that in †*P. encaustus* (e.g., AMNH 754, ROM29043, and UALVP 17658). The antorbital also appears to be similar to that in †*P. encaustus* (e.g., ROM 29043). As in †*P. encaustus*, a supraorbital is absent.

FMNH PF12682 shows a semicircular bone ventral to the anterior portion of the frontal. This bone is here identified as the orbitosphenoid, forming the main part of the dorsal wall of the orbit.

Jaws– The jaws in this species (see Fig. 2-9) are structurally identical with those in †*P. encaustus*. The only differences are: (1) both the upper and the lower jaws are relatively shorter than in †*P. encaustus*; (2) the mouth corner is located at or anterior to the level of the vertical midline of the orbit, whereas in †*P. encaustus*, it is posterior to the level of the posterior edge of the orbit; (3) the dentary bears a coronoid process higher than that in †*P. encaustus*; and (4) teeth on both the dentary and the maxilla number five to eight fewer than in †*P. encaustus.*

The premaxilla is exactly the same as that in †*P. encaustus* in both shape and number of teeth (e.g., AMNH 754, FMNH PF11943, 13035, ROM 29043, UALVP 447, 12712, 17657, 17658, and 17659).

Palato-pterygoid-quadrate Arch– The palato-ectopterygoid (e.g. UALVP 12712) and the endopterygoid (e.g. AMNH 754, UALVP 447, and 17657) are the same as those in †*P. encaustus* in both shape and distribution of teeth.

The quadrate (e.g., on FMNH PF12682, 13035, UALVP 17658, and 17659) is nearly identical with that in †*P. encaustus* in the shape. It has also a "peg-like" head to articulate with the articular in the lower jaw.

Hyoid Arch– A disarticulated hyomandibular can be seen on FMNH PF13035 (mesial view) and UALVP 12712 (lateral view). It differs from that of †*P. encaustus* in having a relatively narrower triangular anterior wing and a shorter opercular process (Fig. 2-13C).

The ceratohyal (FMNH PF12682, ROM 29043, UALVP 12712, 17657, and 17659)

TABLE 2-3: Ratio of depth to width of opercle of †*Phareodus testis*.

SPECIMENS	OPD	OPW	OPD/OPW
AMNH 754	47	21	2.24
AMNH 1336	50	22	2.27
AMNH 2467	36	18	2.00
AMNH 5821	20	9	2.22
AMNH 11547	27	13	2.08
FMNH PF10241	38	19	2.00
FMNH PF10627	25	12	2.08
FMNH PF10960	9	4	2.25
FMNH PF10969	11	5	2.20
FMNH PF11939	11	5	2.20
FMNH PF11941	24	12	2.00
FMNH PF11942	51	25	2.04
FMNH PF11943	25	12.5	2.00
FMNH PF12409	20	10	2.00
FMNH PF12411	28	14	2.00
FMNH PF12412	25	11	2.27
FMNH PF12682	50	25	2.00
FMNH PF26407	42	21	2.00
FMNH PF25014	34	16	2.13
FMNH PF25439	31	13	2.38
FMNH PF13035	22	11	2.00
FMNH PF13576	8	4	2.00
FMNH PF14060	25	11	2.27
UALVP 12712	35	17	2.06
UALVP 17658	59	28	2.11
UALVP 17659	28	14	2.00
AVERAGE			2.12

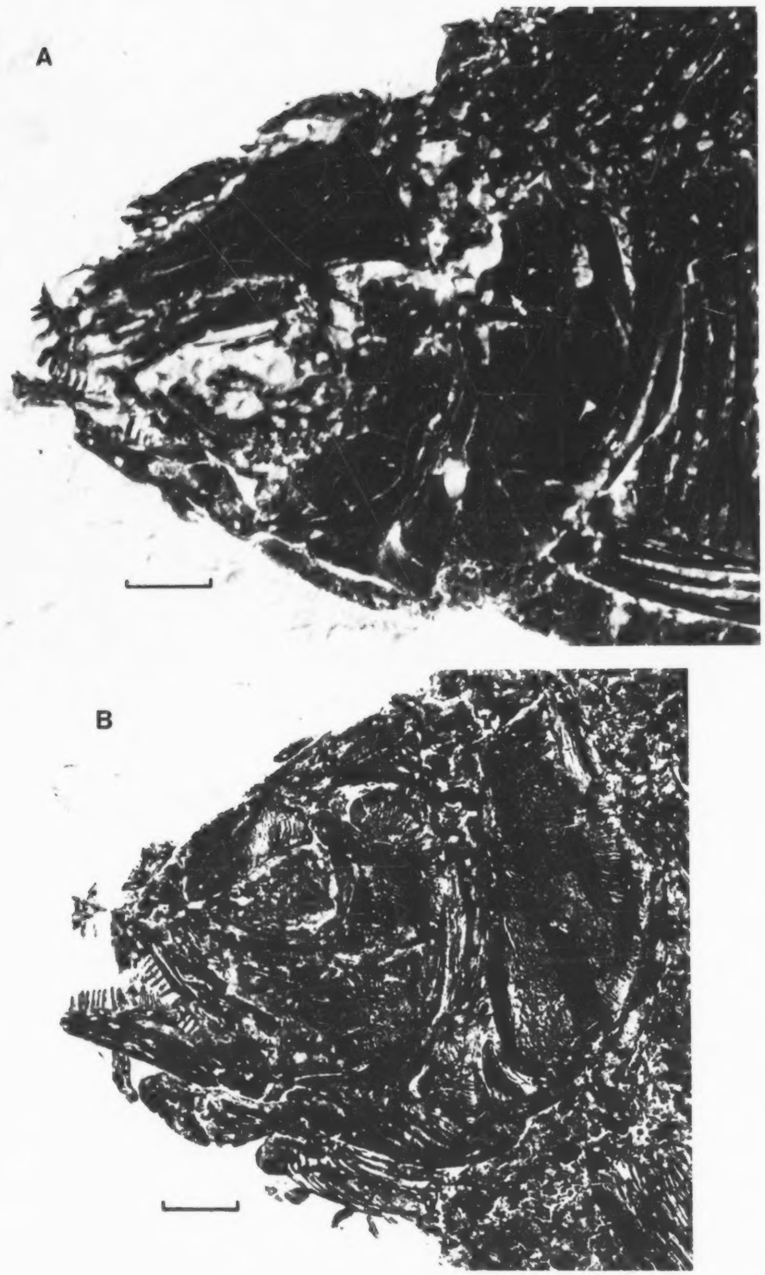

FIGURE 2-8: Photographs of the cranial skeleton of †*Phareodus testis*. **A**, FMNH PF14062, scale bar equals 5mm. **B**, FMNH PF12682, scale bar equals 10mm.

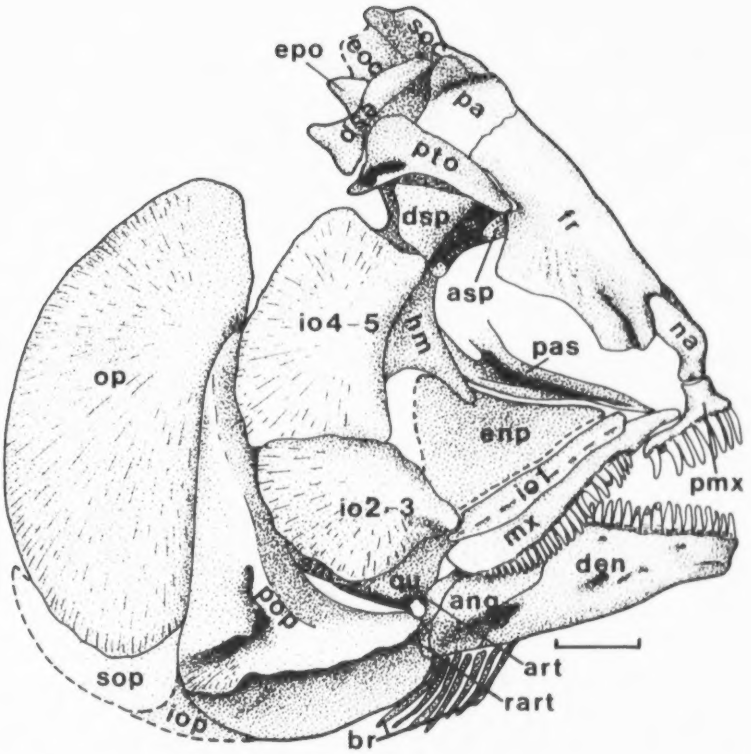
epo
eoc
soc
pa
dfa
pto
dsp
fr
asp
io4–5
hm
pas
na
op
enp
io1
pmx
io2–3
mx
den
qu
ang
pop
art
rart
sop
iop
br

FIGURE 2-9: Partial restoration of the cranial and opercular skeleton of †*Phareodus testis* based on UALVP 17658. Scale bar equals 10mm.

and the fused basihyal-basibranchial tooth plate (FMNH PF13035, UALVP 17657, and 17658) are indistinguishable from those of †*P. encaustus*.

In total, nine to 12 slender branchiostegals are present; however, most of the specimens have 10, as in †*P. encaustus* (Table 2-4A-B).

Cephalic lateral line system– A comprehensive survey of the cephalic lateral line system on AMNH 744, FMNH PF10241, 11943, 12682, 13035, 14062, ROM 29043, UALVP 447, 17658, and 17659 suggests that this system conforms to the same pattern as that in †*P. encaustus*. The supraorbital canal ends posteriorly also only in the frontal.

Pectoral Girdle and Fin– Well-preserved but disarticulated cleithrum, coracoid, and scapular are seen on UALVP 12712. These bones are identical with those of †*P. encaustus* in their general appearance. So are the supracleithrum (e.g., FMNH PF11943, 26407, UALVP 12712, and 17657) and the posttemporal (e.g., FMNH PF11942, 11943, 13035, 26407, UALVP 447, 12712, and 17658). Nothing is known about the postcleithrum.

The pectoral fin consists of seven to 10 rays (Table 2-4A-B), just as in †*P. encaustus*, with the first pectoral ray particularly strong and long, extending posteriorly to beyond the pelvic fin.

Pelvic Girdle and Fin– The pelvic girdle is the same as that in †*P. encaustus*. The small pelvic fin consists also of five to six (on most of the specimens) distally segmented and branched rays (Table 2-4A-B). The distance between the pelvic and the pectoral fins is also at least 1.5 times the distance between the pelvic and the anal fins.

Dorsal and Anal Fins– Both the dorsal and anal fins are rounded in outline and posteriorly located. As in †*P. encaustus*, the beginning of the dorsal fin is posterior to the begining of the anal fin externally. Internally, however, both the first dorsal pterygiophore and the first anal pterygiophre join with the first caudal vertebrae (the last preural) respectively via the neural and the haemal spines, confirming that both the dorsal and the anal fins begin internally from the same vertebrae.

Vertebral Column– The meristic characters related to the vertebral column (number of precaudal and caudal vertebrae, and supraneurals) of †*P. testis* are similar to those of †*P. encaustus* (Table 2-4A-B). So are the morphological characters. The only difference is that the abdominal part of the vertebral column is less dorsally arched in †*P. testis* than in †*P. encaustus*.

Caudal Skeleton and Fin– A well-preserved caudal skeleton is shown on AMNH 2799, FMNH PF11943, and UALVP 12712 (Fig. 2-6B). It is essentially the same as that in †*P. encaustus*. The only differences are: (1) the neural spines on the first and second

TABLE 2-4A: Meristics of †*Phareodus testis* in collections of AMNH and FMNH.

	PCV	CV	TV	BR	PFR	VFR	DFR	DP	AFR	AP	CFR	H	EP	SPN	NSU1	NSPU2	UN
AMNH 743	23	27	50	9	9	5	19	20	24	24	17	?	?	22	?	1	0
AMNH 805	25	24	49	?	?	5	18	19	25	24	17	6	1	24	2	2	0
AMNH 1336	23	26	49	8	8	4	18	19	27	28	17	6	1	?	2	1	0
AMNH 2467	23	26	49	11	9	6	?	18	25	26	17	6	1	22	2	2	0
AMNH 2471	25	27	52	?	9	5	19	20	24	25	17	5	1	26	2	1	0
AMNH 2799	22	25	47	?	?	5	18	19	25	26	17	6	1	?	2	1	0
AMNH 5821	24	26	50	10	8	4	16	18	25	26	17	6	1	24	2	1	0
AMNH 6301	24	25	49	?	?	4	19	20	27	28	17	6	1	24	2	2	0
AMNH 8124	?	26	?	?	9	6	17	18	26	26	17	6	1	?	2	1	0
AMNH 11547	23	25	48	10	9	4	18	19	26	27	17	5	1	22	2	2	0
FMNH PF10627	22	26	48	9	9	6	20	20	26	26	17	6	1	22	2	1	0
FMNH PF10960	24	27	51	10	7	5	18	20	26	27	17	5	1	24	2	2	0
FMNH PF10969	22	27	49	10	8	6	19	19	26	27	17	6	1	?	2	1	0
FMNH PF11939	23	25	48	9	9	5	17	18	26	26	?	6	1	23	2	1	0
FMNH PF11941	?	26	?	?	?	?	19	20	27	26	17	6	1	?	2	1	0
FMNH PF11942	24	25	49	?	8	6	20	21	28	27	17	6	1	24	2	1	0
FMNH PF11943	23	24	47	10	7	6	18	19	26	26	17	6	1	23	2	2	0
FMNH PF12409	25	26	51	9	7	6	20	21	24	25	17	6	1	26	2	1	0
AVERAGE	24	26.5	50.5	9	8	5.5	19.5	20.5	24	24.5	17	6	1	24	2	1	0

TABLE 2-4B: Meristics of †*Phareodus testis* in collections of FMNH, ROM, and UALVP.

	PCV	CV	TV	BR	PFR	VFR	DFR	DP	AFR	AP	CFR	H	EP	SPN	NSU1	NSPU2	UN
FMNH PF12411	22	26	48	11	8	6	18	19	25	26	18	5	1	22	2	1	0
FMNH PF12412	?	?	?	9	9	6	20	20	25	26	17	6	1	?	2	1	0
FMNH PF12682	23	27	50	10	7	?	20	20	27	28	17	6	1	23	2	2	0
FMNH PF13035	23	26	49	9	9	6	18	19	26	27	17	6	1	23	2	1	0
FMNH PF13576	24	25	49	10	7	5	17	18	25	26	16	6	1	23	2	1	0
FMNH PF14061	?	?	?	?	?	?	18	19	28	28	17	?	?	?	?	?	?
FMNH PF25439	?	27	?	?	7	6	18	19	26	26	17	6	1	?	2	2	0
FMNH PF25014	23	28	51	12	7	6	18	19	26	26	17	6	1	24	2	1	0
FMNH PF26407	24	27	51	9	7	6	18	19	26	26	16	6	1	25	2	2	0
ROM 28560	23	26	49	8	9	5	18	19	25	25	17	5	1	23	2	1	0
ROM 29076	23	26	49	?	?	?	19	20	27	28	17	?	?	?	?	?	?
UF 31	24	24	48	?	9	6	18	19	25	26	17	6	1	24	2	1	0
UALVP 447	25	26	51	10	10	6	18	21	25	26	17	?	?	25	?	?	?
UALVP 17657	23	26	49	10	10	6	19	20	28	27	17	6	1	23	2	2	0
UALVP 17658	24	25	49	9	8	6	21	21	26	26	17	?	?	23	?	?	?
UALVP 17659	25	26	51	12	10	6	18	20	25	26	17	?	?	25	?	?	?
AVERAGE	23.5	26	49.5	11.5	9	6	18	19.5	25	26	17.5	5	1	23.5	2	1	0

preurals may be double in †P. *testis*, rather than single as in †*P. encaustus*; (2) the preurals taking part in supporting the lower lobe of the caudal fin decrease to three in †*P. testis*, whereas in †*P. encaustus*, four preurals may take part in supporting the lower lobe of the caudal fin.

As in †*P. encaustus*, all the specimens but FMNH PF13576 examined for this study have a caudal fin consisting of 17 principal rays (i-8-7-i), of which nine are in the lower lobe, and eight in the upper lobe. FMNH PF13576 is the only exception, having 16 principal rays in its caudal fin, of which nine are in the lower lobe, and seven in the upper lobe.

Scales– The scales in †P. *testis* are indistinguishable from those in †*P. encaustus*.

DISCUSSION

i. Two valid North American †*Phareodus* species

The above descriptions of †*Phareodus encaustus* and †*P. testis* based on the new materials from the Green River Formation strongly suggest that there are only two valid North American †*Phareodus* species, agreeing with Grande's (1984) assertion. Overwhelmingly these two species are strikingly similar to each other in meristics and postcranial characters, including the structures of the caudal skeleton. Grande (1984) listed the main diagnostic differences between the two North American †*Phareodus* species. Most of them, with the exception only of the meristics of the dorsal and anal fins, have been proved to overlap based on the new specimens from the Green River Formation (Table 2-5); if so, they are of little use for taxonomy. I find that the two North American †*Phareodus* species differ from each other mainly in the following cranial skeletal characters.

1. Anterior portion of frontal broader in †*Phareodus encaustus* than in †*P. testis*: Although both †*Phareodus encaustus* and †*P. testis* have a pair of frontals that are anteriorly broader than posteriorly, the anterior portion of the frontal in †*Phareodus encaustus* is much more laterally expanded than in †*P. testis*, with the broadest anterior width to posterior width ratio at least 2 (Fig. 2-2A). In contrast, the frontal on most of the specimens of †*P. testis* does not have an extremely laterally expanded anterior portion; its maximum anterior width is about 1.5 times its posterior width. On some of the specimens referred to †*P. testis* in this chapter, the frontal is only slightly broader anteriorly than posteriorly.

2. Parietal longer in †*Phareodus encaustus* than in †*P. testis*: Proportionally, the parietal length to the frontal length differs between †*Phareodus encaustus* and †*P. testis*. I find a value of 1:3-3.5 in †*Phareodus encaustus* and a value of 1:5 in †*P. testis*. Therefore, the parietal in †*Phareodus encaustus* is relatively longer than in †*P. testis.*

3. Horizontal arm of preopercle in †*Phareodus encaustus* shorter than in †*P. testis*: As shown in Figs. 2-3 and 2-5D, the preopercle in †*Phareodus encaustus* is curved with an indistinct horizontal arm. This type of preopercle is seen on all the new materials of †*Phareodus encaustus* with this bone preserved. However, the preopercle in †*P. testis* differs in having a distinct horizontal arm that is about 3/5 the length of the vertical arm and a protruding, rounded postero-ventral corner (see Figs. 2-8B and 2-9).

4. Posterior infraorbitals longer than deep in †*Phareodus encaustus* but deeper than long in †*P. testis*: The two posterior infraorbitals of †*Phareodus encaustus* are quite different from those of †*P. testis* in detail. In †*Phareodus encaustus,* they are longer than deep, forming a relatively longer cheek region than in †*P. testis*. The upper one, which is thought to be the fused io4-5, is twice as deep as the lower one, with its anterior edge forming the whole posterior edge of the orbit. The lower one is somewhat elongate, twice as long as deep, with a convex dorsal edge and a distinctly contracted anterior end that forms the postero-ventral edge of the orbit (see Figs. 2-3 and 2-11B).

However, the two posterior infraorbitals in †*P. testis* are shorter than deep; they thus compose a short cheek region. The upper one (io4-5) is less than 1.5 times the depth of the lower one. The lower one (io2-3) is more or less trapezoidal and usually deeper than long. Both the upper and lower posterior infraorbitals take part in the formation of the posterior edge of the orbit (see Figs. 2-8, 2-9, and 2-11C).

5. Lengthened lower and upper jaws in †*Phareodus encaustus*: Almost all previous authors noticed the difference of the maxilla and dentary tooth numbers between the two North American †*Phareodus* species (Leidy, 1873; Cope, 1877b, 1883; Thorpe, 1938, Roellig, 1967; Grande, 1984). In fact, the numbers of teeth on the jaws is in direct proportion to the lengths of the jaws. †*Phareodus encaustus* has lengthened jaws, in which the maxilla extends back nearly to the level of the quadrate condyle, ending posteriorly far behind the posterior edge of the orbit. The lower jaw reaches to the level of the postero-ventral corner of the elongate third infraorbital.

The jaws in †*P. testis* are obviously shorter than in †*P. encaustus*; the maxilla extends posteriorly only to the level of the middle or posterior 1/3 of the orbit. The lower jaw ends posteriorly beneath the posterior edge of the orbit. This difference of jaw length is considered to be one of the most important features for distinguishing between these two species.

6. Mouth corner more posteriorly located in †*Phareodus encaustus* than in †*P. testis*: It is evident that the position of the mouth corner is closely related to the length of the jaws. Since †*Phareodus encaustus* has lengthened lower and upper jaws, the mouth cleft (gape) in this species is much deeper than that in †*P. testis*, with the corner of the gape extending posteriorly to beyond the level of the second infraorbital or the posterior edge of the orbit (e.g., Figs. 2-1 and 2-3). In contrast, the mouth cleft in †*P. testis* is shallow in comparison. Its corner is located anterior to the posterior edge of the orbit, or, in most cases, anterior to the vertical mid-line of the orbit (see Figs. 2-8 and 2-9).

7. Hyomandibular with more expanded triangular anterior wing in †*Phareodus encaustus* than in †*P. testis*: Although the hyomandibulars in the two valid North American †*Phareodus* species look alike in having a stick-like opercular process, they can be discriminated by the appearance of the anterior extension. In †*Phareodus encaustus*, the anterior part is greatly extended to form an expanded triangular wing (e.g., Fig. 2-13B). However, in †*P. testis*, this bone has only a narrow subtriangular anterior portion (see Fig. 2-13C).

The development of an expanded triangular anterior wing coincides with the lengthening of the cheek region. As discussed above, the cheek region in †*Phareodus encaustus* is relatively longer than in †*P. testis*. This lengthening of the cheek region results in the enlargement of the space between the palatopterygo-quadrate arch and the hyoid arch. The enlarged space between the two arches is filled by the hyomandibular, the key element linking the palatopterygo-quadrate arch with the hyoid arch.

These seven visible differences between the cranial skeletons of †*Phareodus encaustus* and †*P. testis* strongly confirm the validity of these two North American †*Phareodus* species.

Among previously named fossil osteoglossomorphs, †*Brychaetus muelleri* Woodward (1901), †*Musperia radiata* (Heer) Sanders (1934), †*Phareoides queenslandicus* (Hills) Taverne (1973), and †*Phareodusichthys tavernei* Gayet (1991) were considered to have some relationships with the North American †*Phareodus*. My recent examination indicates that †*Brychaetus muelleri* is more similar to †*Phareodus encaustus* in the preserved cranial skeletal features (see Roellig, 1967, 1974; Taverne, 1978). Further investigation will be needed to confirm whether there is a close relationship between thses two species, or whether †*Brychaetus* Woodward (1901) is a junior synonymy of †*Phareodus* Leidy (1873) (see Chapter 7).

†*Musperia radiata* appears to be more or less comparable with †*Phareodus testis* in the length of the jaws, the position of the mouth corner, and the meristics of the anal fin rays and anal pterygiophores, suggesting that it might be synonymous with †*Phareodus*. However, at present, the evidence is far from sufficient to prove the possible relationship between †*Musperia radiata* and †*Phareodus testis*.

†*Phareoides queenslandicus* was originally named as †*Phareodus queenslandicus* (Hills, 1934). My study of materials referred to †*Phareoides queenslandicus* synonymizes †*Phareoides* with †*Phareodus*, by suggesting that †*Phareodus queenslandicus* (Hills, 1934) is most closely related to †*Phareodus encaustus* in cranial skeletal characters (see the discussion in the following section).

†*Phareodusichthys tavernei* was recently named by Gayet (1991) based on poorly preserved premaxilla and dentary from the Santa Lucia Formation (Paleocene) of Tiupampa, Bolivia. From the picture and the description of the premaxilla, this South American fossil osteoglossid seems to be another possible relative of the North American †*Phareodus*. So far as I know, in all the named osteoglossomorphs, a "spike"-shaped premaxilla bearing 7-9 teeth is only seen in †*Phareodus* (see Fig. 2-4) and †*Phareodusichthys*. Future study of †*Phareodusichthys tavernei* may provide more important information about the phylogeny of Osteoglossinae.

ii. Notes on Systematics of †*Phareoides queenslandicus* (Hills)

1. Synonymy of †*Phareoides* with †*Phareodus*– When Taverne (1973) established †*Phareoides*, he used 20 characters in its diagnosis:

> "(1) Ostéoglossidé de grande taille (50 cm), au corps court et trappu; (2) mâchoires ornées de grandes dents; (3) supraethmoïde hypertrophié; (4) naso-frontaux en contact médian; (5) expansions latérales externes de grande dimension dans la région naso-frontale; (6) pariétaux en contact médian et dénivelés en leur milieu; (7) ptérotiques étroits et très longs; (8) présence d'une fosse occipito-dorsale sur le pariétal, l'épiotique et le supraoccipital; (9) un supramaxillaire; (10) ptérygoïdes dentés; (11) hypertrophie des troisiéme et quatriéme infraorbitaires; (12) préoperculaire haut et large, à branche ventrale très réduite; (13) operculaire étroit mais très haut; (14) museau raccourci; (15) mandibule large et remontante; (16) premier rayon pectoral beaucoup plus fort que les suivants; (17) nageoires dorsale et anale très reculée sur le corps; (18) une cinquantaine de vertèbres; (19) vertèbres abdominales à grandes hémapophyses situées transversalement; (20) écailles grandes, ornées d'une

fine granulation et à radii en structure réticulée."

Among the above features of †*Phareoides*, none can be designated as an autapomorphy of this genus in the family Osteoglossidae. Character (1) is present not only in †*Phareodus*, but also in the Recent *Osteoglossum*, *Scleropages*, and *Heterotis*, if we count both the juveniles and the adults. Moreover, such variation in body size is of doubtful significance because we do not know how large the largest individuals of this Australian fossil species could be.

Character (2) is definitely a plesiomorphy. It is present in all of the extant and fossil genera of Osteoglossiformes (Ridewood, 1904, 1905; Taverne, 1977, 1978, 1979) except †*Singida* (see Greenwood and Patterson, 1967). Large teeth on the lower and upper jaws can also be seen in most of the genera of Hiodontiformes (e.g. †*Yanbiania* Li, 1987; †*Eohiodon* Cavender, 1966; and *Hiodon*) and many other teleosts (see Gregory, 1933).

Character (3) needs to be clarified. Taverne's hypertrophied "supraethmoïde" [synonymous with Hills' (1934) "mesethmoid" or Kershaw's (1976) "dermethmoid"] is in fact shared at least by the two North American †*Phareodus* species. It should also be noted that Taverne's restoration of the naso-ethmoid region and his identification of the bones in this region of †*Phareodus acutus* [=†*Phareodus encaustus* (Cope) 1872] is incorrect. There is no such bone as the "supraethmoïde" at the position labelled by Taverne (1973: p. 498, fig. 1) in either †*Phareodus encaustus* or †*P. testis*. His so-called "nasal" is also likely misidentified. Where Taverne labelled a "nasal," I can find only one bone that shows an appearance similar to his so-called "supraethmoïde" in †*Phareoides queenslandicus* (see Fig. 2-10A). The true nasals, which could have been either missing from the specimens (e.g. FMNH PF14262) or disarticulated with the adjacent bones (e.g. FMNH PF12683), are separated from each other by the subrhomboid mesethmoid in the two North American †*Phareodus* species (see Figs. 2-3 and 2-9). I am also doubtful of Taverne's (1973, 1974, 1978) restoration of †*Brychaetus muelleri* (see Woodward, 1901). Judging from the illustrations provided by Woodward, that western European species may be also similar to the two North American †*Phareodus* species in the above aspects (pers. obs.).

Characters (4) and (5) are also in need of clarification. Hills (1934) made a mistake in identifying the frontal as the fused nasal plus frontal and labeling the anterior extension of the frontal as the "nasal" of †*Phareodus queenslandicus*. Taverne (1973, 1978) modified Hills' usage, but he continued labeling the frontal and nasal as a fused "naso-frontaux" when he established †*Phareoides*. My study of the cast of UQ F14960 suggests that the nasals are missing from the specimen, leaving only a "V-shaped" depression on the anterior margin of each of the frontals, and that two nasals are also separated from each other by the mesethmoid in this fish. The part labeled as the "nasal" by Taverne is, therefore, the medio-anterior extension of the frontal (Fig. 2-10A). This situation is identical with that in the two North American †*Phareodus* species (Figs. 2-2A, 2-3 and 2-9). Therefore, Taverne's so-called "naso-frontaux" of †*Phareoides queenslandicus* consist only of the frontals. As illustrated by Taverne himself, the frontals in †*Phareodus encaustus* and †*Brychaetus muelleri* are also medially sutured with each other and antero-laterally expanded. These two characters can thus only be considered to be synapomorphies shared by †*Phareodus*, †*Brychaetus*, and †*Phareoides*.

Character (6) is definitely not unique to †*Phareoides*. Parietals meeting with each other along the dorso-medial line can be seen at least in †*Phareodus*, †*Brychaetus*, the extant *Heterotis*, *Arapaima*, notopterids (Ridewood, 1904, 1905; Kershaw, 1976; Taverne, 1978), and all lycopterids and hiodontids (Ridewood, 1904; Greenwood, 1970; Taverne, 1977, 1978; Ma, 1980, 1986, 1987; Li, 1987; also see chapters 5-6 in this thesis). The only difference is that the suture between the two parietals is zigzag-shaped in †*Phareoides* but nearly straight in the other genera mentioned above.

Character (7) refers to the pterotics. Although they are incompletely preserved on the specimen (Fig. 2-10A), the pterotics of †*Phareoides* are indistinguishable from those of the two North American †*Phareodus* species (Figs. 2-2A, 2-3, 2-8, and 2-9)). In addition, elongate pterotics can also be seen in †*Brychaetus* (Woodward, 1901; Roellig, 1974; Taverne, 1978) and in the extant *Arapaima* (Ridewood, 1905; Kershaw, 1976). It is evident that this character is not unique to †*Phareoides*.

Character (8) defines a dorso-occipital fossa on the parietal, epiotic, and supraoccipital of †*Phareoides*. A similar depression is also developed in †*Brychaetus* (Taverne, 1978) and the two North American †*Phareodus* species (see Figs. 2-2A, 2-3 and 2-9)).

Character (9) suggests the presence of one supramaxilla in †*Phareoides*. My examination failed to confirm this bone in the specimens referred to †*Phareoides*. I believe Taverne's so-called "supramaxillaire" could be the posterior part of the endopterygoid.

Character (10) is related to the palato-pterygo-quadrate arch. In both the fossil and the extant osteoglossomorphs, toothed pterygoids (including ectopterygoid and endopterygoid) are commonly seen in most of the taxa of Osteoglossomorpha (Greenwood et al., 1966; Taverne, 1977, 1978). Therefore, †*Phareoides* can not be characterized by this plesiomorphy.

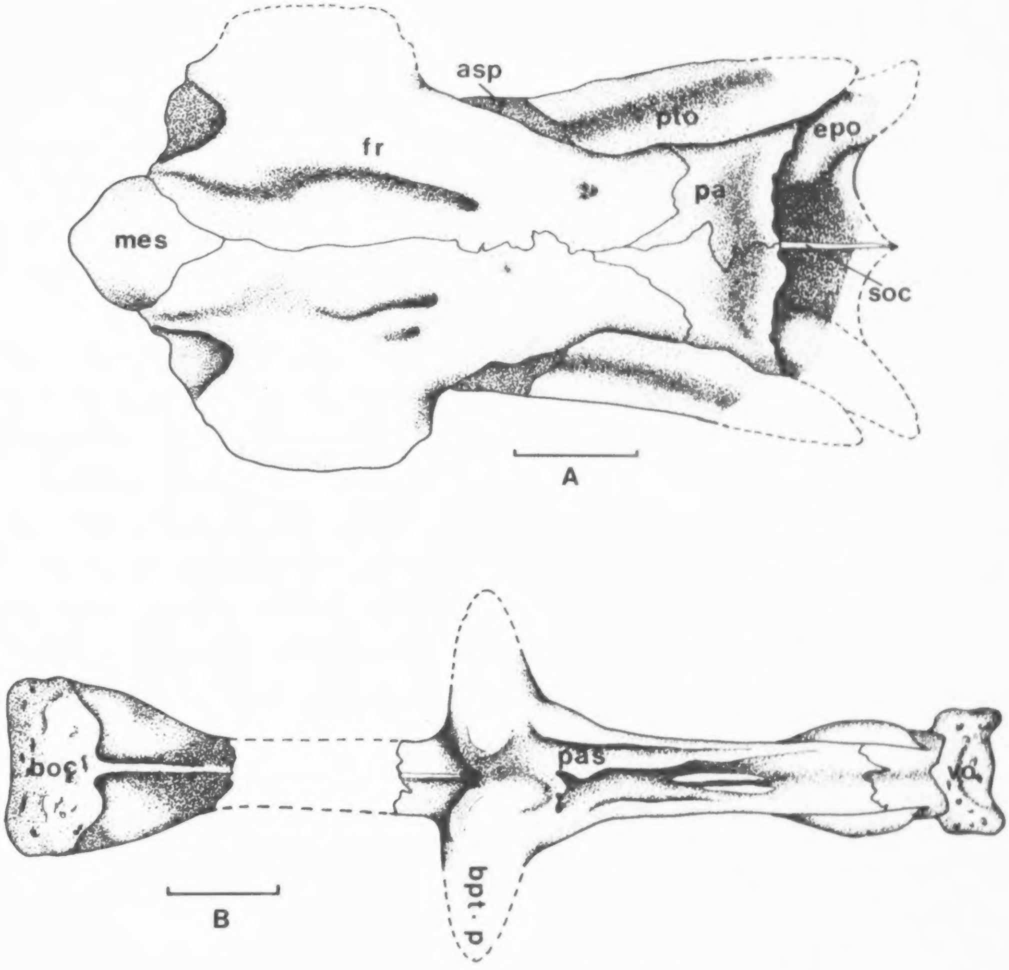

FIGURE 2-10: Partially restoration of the cranial skeleton of †*Phareodus queenslandicus*. **A**, skull roof, based on QMF 2917, the cast of F14960 of the University of Queensland. Note the "v-shaped" depression on the anterior margin area of each of the frontals, which receives the posterior end of the nasal in the two North American †*Phareodus* species as shown in Figs. 2-3 and 2-9. **B**, middle ventral part of the cranial base, based on QMF 2359a. Scale bars equal 10mm.

Character (11) describes the posterior infraorbitals of †*Phareoides*. In fact, †*Phareodus encaustus* shares this character with †*Phareoides* (Fig. 2-11A-B). Similar posterior infraorbitals may also be seen in †*Brychaetus* (Woodward, 1901; Roellig, 1967, 1974; Taverne, 1978).

Characters (12) and (13) define the preopercle and opercle of †*Phareoides*. Using these two characters, I am not able to distinguish †*Phareoides* from any of the other genera grouped in the Osteoglossinae.

Character (14) is doubtful because the naso-oral region is poorly preserved on the specimens. Even if Taverne is correct, a reduced (short) naso-oral region can also be seen in the two North American †*Phareodus* species and the extant *Heterotis*.

Character (15) refers to the lower jaw. A detailed comparison suggests that the mandibular in †*Phareoides* is almost identical with that in the two North American †*Phareodus* species in both structure and shape (Fig. 2-12).

Character (16) is one of the synapomorphies of the subfamily Osteoglossinae (Chapter 3). Including †*Singida* (see Greenwood and Patterson, 1967), all of the genera in the subfamily have a particularly strong first pectoral fin ray.

Character (17) is plesiomorphic for Osteoglossidae. Posteriorly located dorsal and anal fins are present in many Osteoglossomorpha.

Character (18), which gives the number of the vertebrae of †*Phareoides*, and (19), which defines the parapophyses, are shared also by the two North American †*Phareodus* species. My examination indicates that †*Phareodus encaustus* and †*P. testis* also have a vertebral column consisting of 47 to 51 centra (Table 2-5) and strong parapophyses on the abdominal vertebrae.

Character (20) describes the scales of †*Phareoides*. Reticulate scales with fine granular ornament are seen in all of the extant genera of Osteoglossidae (Lauder and Liem, 1983; Greenwood et al., 1966; Taverne, 1977, 1978) and in fossil †*Phareodus* (Cope, 1872, 1873; Leidy, 1873; Thorpe, 1938; Grande, 1984) and †*Sinoglossus* (Su, 1986).

To sum up, Taverne's diagnosis for †*Phareoides* does not characterize that genus. It is only a list of characters of †*Phareodus* mixed with characters of the family Osteoglossidae, the superorder Osteoglossomorpha, and other primitive teleosts. In fact, †*Phareoides* and †*Phareodus* are indistinguishable from each other in all of the 20 characters.

2. Phylogeny of †*Phareodus queenslandicus*– Grande's (1984) study and my recent reexamination suggest that †*Phareodus* contains only two valid North American

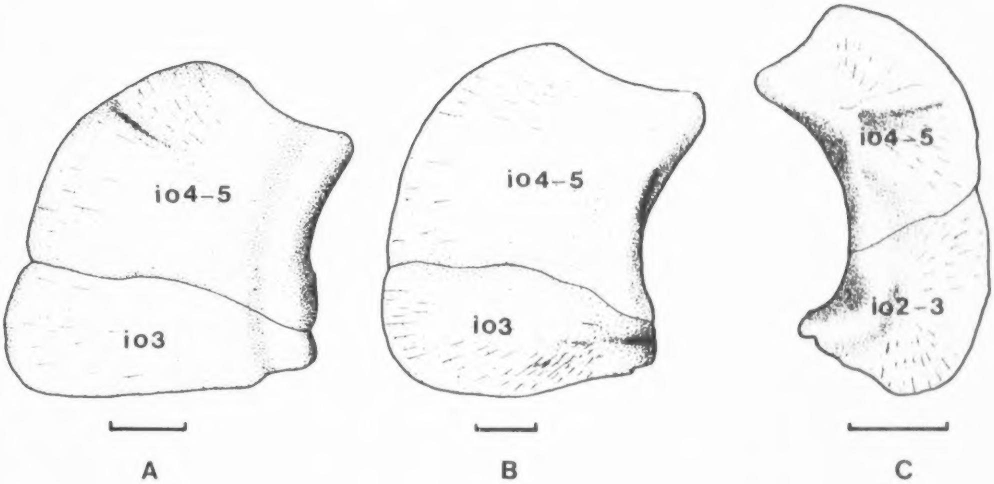
io4–5
io3
A
io4–5
io3
B
io4–5
io2–3
C

FIGURE 2-11: Comparison of the posterior infraorbitals in †*Phareodus*. **A**, †*Phareodus queenslandicus*, drawn from QM F2357. **B**, †*Phareodus encaustus*, from FMNH PF10256. **C**, †*Phareodus testis*, based on FMNH PF12682. Scale bars equal 10mm.

species: †*Phareodus encaustus* and †*P. testis*. The difference between these two North American species seems to be greater than the difference between †*Phareodus queenslandicus* and †*P. encaustus* (see Table 2-5). Moreover, †*Phareodus queenslandicus* appears to be phylogenetically more closely related to †*P. encaustus* than it is to †*P. testis*. This hypothesis is supported by the following character states.

1) Anterior portion of frontal greatly expanded laterally. The frontal in †*Phareodus queenslandicus* is almost identical to that in †*Phareodus encaustus* in the shape. In these two species the frontal has an anterior portion that is greatly expanded laterally, with a width at least twice as great as that of the posterior portion, or 1/2 of the length of this bone (see Fig. 2-2A and 2-10A). A frontal similar to that in †*Phareodus queenslandicus* and †*Phareodus encaustus* was supposed to be present in †*Brychaetus muelleri* by Roellig (1967, 1974) and Taverne (1978). My study suggests that there are too many discrepancies between Taverne's restorations and Woodward's (1901) original illustrations for that species. That makes me doubtful about Taverne's description of the frontal in †*Brychaetus muelleri*.

It is true that the frontals in some other osteoglossiforms (Greenwood and Patterson, 1967; Roellig, 1967; Kershaw, 1976; Taverne, 1977, 1978; Grande, 1984) are also anteriorly broader than posteriorly; however, none of them has an anterior portion twice as broad as the posterior portion (pers. obs.).

2) Hyomandibular with a long stick-like opercular process and a broad subtriangular anterior wing. Among the previously named fossil osteoglossids, such a hyomandibular has been seen so far only in †*Phareodus queenslandicus* (QM F2359 = RP/B-1 in Hills, 1934) and †*Phareodus encaustus* (Fig. 2-13A-B). The stick-like opercular process in these two species is particularly long and forms an approximately equal angle with the lower vertical ridge of the hyomandibular. The subtriangular anterior wing extends anteriorly to the posterior edge of the orbit, ending in a distinct process that connects with the endopterygoid. In contrast, in †*P. testis*, the hyomandibular bears a shorter stick-like opercular process and a narrow subtriangular anterior wing.

3) Dentary bearing nearly the same number of teeth. As shown in Figs. 2-4 and 2-12, the dentary in both †*Phareodus queenslandicus* and †*P. encaustus* bears 27 large conical teeth. This coincidence can not be interpreted as a simple similarity between these two species. Most of the specimens referred to †*Phareodus encaustus* have 25 to 27 dentary teeth. This is also the estimate of the number of dentary teeth in †*Phareodus queenslandicus*. The teeth on the dentary of †*P. testis* are usually three to four fewer

TABLE 2-5: Comparison of the meristic characters among †*Phareodus* species.

	†Phareodus encaustus	***†Phareodus testis***	***†Phareodus queenslandicus***
PCV	22 - 25 (mainly 23)	22 - 25	~23
CV	25 - 27 (mainly 26)	24 - 28	~26
TV	47 - 51 (mainly 49)	47 - 52	~49
BR	9 - 10 (mainly 10	8 - 11	?
PFR	7 - 10	7 - 10	~ 6
VFR	4 - 6	4 - 6 (mainly 6)	~ 4
DFR	17 - 22	16 - 20 (mainly 18)	~19
DP	18 - 24	18 - 21 (mainly 19	~19
AFR	22 - 25	24 - 28 (mainly 26)	~26
AP	22 - 26	24 - 28 (mainly 26)	~26
CFR	17	17 (16 on FMNH PF13576)	16
H	5 - 6 (mainly 5)	5 - 6 (mainly 6)	?
EP	1	1	?
SN	22 - 26	22 - 26	?
nu1	2	2	?
npu2	1	1 - 2	?
un	0	0	?
OPD/OPW	2 - 2.50	2 - 2.38	2 - 2.50

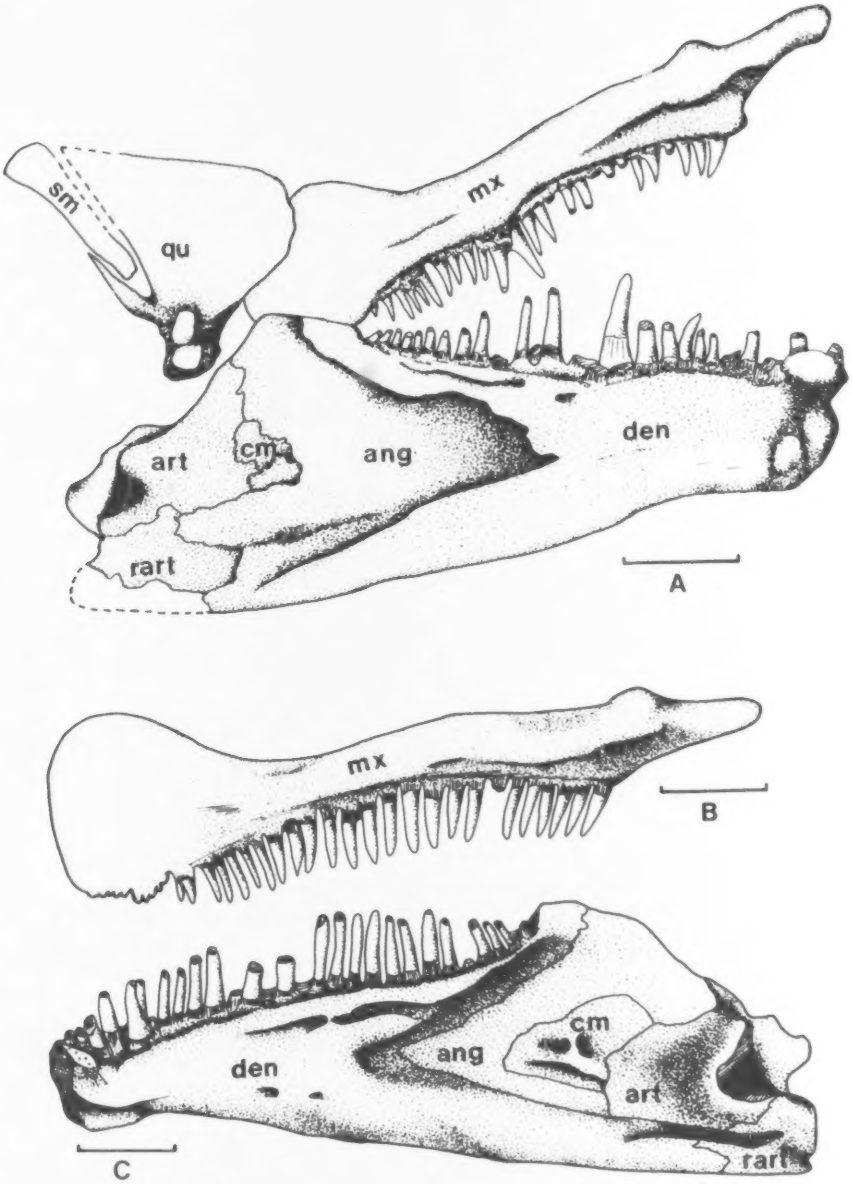
sm
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FIGURE 2-12: Comparison of the jaws of †*Phareodus queenslandicus* with those of †*Phareodus encaustus*. **A**, †*Phareodus queenslandicus*, drawn from QM F2357. **B**-**C**, †*Phareodus encaustus*, **B** is based on FMNH PF12683, and **C** on AMNH 2472. Scale bars equal 10mm.

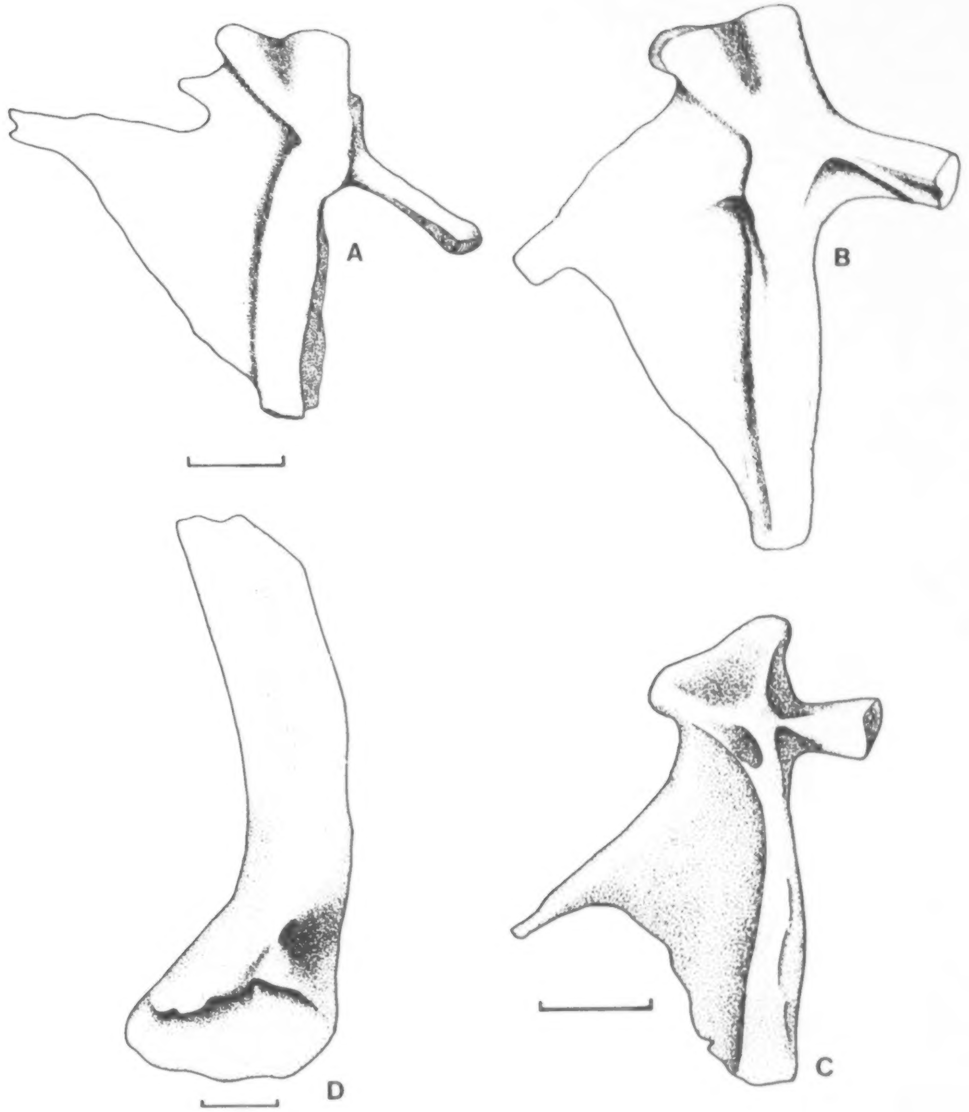

FIGURE 2-13: Showing the hyomandibular of three †*Phareodus* species and the preopercle of †*Phareodus queenslandicus*. **A**, hyomandibular of †*P. queenslandicus*, based on QM F2359a; **B**, hyomandibular of †*P. encaustus* , drawn from FMNH PF10285); and **C**, hyomandibular of †*P. testis* , from FMNH PF13035). **D**, preopercle of †*P. queenslandicus,* based on QMF 2359a. Scale bars for **A**, **B** and **D** equal 10mm, for **C** 3mm.

than those of the above two species. It seems to me that the number of dentary teeth may be phylogenetically informative although this significance should be further investigated.

4) Preopercle with an indistinct horizontal arm. In †*Phareodus queenslandicus*, the preopercle is moderately curved, with the upper part approximately as broad as the lower part (Fig. 2-13D). No distinct horizontal arm can be seen in this species. This type of preopercle is basically the same as that in †*Phareodus encaustus* (Fig. 2-5D). Although the preopercles in †*P. testis* (e.g. UALVP 17658) and the extant *Osteoglossum* (e.g. UAMZ 4642) are also shallowly curved in shape, they possess a distinct horizontal arm and a dorsally tapered vertical arm. Thus a moderately curved preopercle without a distinct horizontal arm may be another important derived character state linking †*Phareodus queenslandicus* with †*P. encaustus.*

5) Posterior infraorbitals (io3 and io4-5) in the same pattern. QMF 2357 (Fig. 211A) and F5754 show two posterior infraorbitals of †*Phareodus queenslandicus*. The narrower lower one was considered to be the third infraorbital, and the broader upper one the fourth by Taverne (1978, p. 26, fig. 15). Among the other known osteoglossomorphs (see Nelson, 1969), similar posterior infraorbitals are present only in †*P. encaustus* and possibly in †*Brychaetus* (pers. obs.). As shown in Figures 2-3 and 2-11A-B, †*Phareodus queenslandicus* and †*P. encaustus* are indistinguishable from each other in having the same pattern of the posterior infraorbitals.

Other character states that may also support a closest relationship between †*Phareodus queenslandicus* and †*P. encaustus* are from the dorsal fin, the dermopterotic (QM F2917, cast of UQ F14960), and the upper jaw (QM F2357).

All the above evidence indicate that †*Phareoides* Taverne 1973 is a junior synonym of †*Phareodus* Leidy 1873.

CONCLUSIONS

1. †*Phareodus encaustus* and †*P. testis* are two valid North American †*Phareodus* species. These two species differ one from another mainly in the following cranial skeletal features: (1) anterior portion of frontal much broader in †*Phareodus encaustus* than in †*P. testis*, (2) parietal longer in †*Phareodus encaustus* than in †*P. testis*, (3) horizontal arm of preopercle shorter in †*Phareodus encaustus* than in †*P. testis*, (4) posterior infraorbitals longer than deep in †*Phareodus encaustus* but deeper than long in

†*P. testis*, (5) lower and upper jaws longer in †*Phareodus encaustus* than in †*P. testis*, (6) mouth corner more posterior located in †*Phareodus encaustus* than in †*P. testis*, (7) hyomandibular with a more expanded triangular anterior wing in †*Phareodus encaustus* than in †*P. testis*.

2. Taverne's diagnosis for †*Phareoides* is only a list of characters of †*Phareodus* mixed with characters of the family Osteoglossidae and the superorder Osteoglossomorpha. In fact, †*Phareoides* and †*Phareodus* are indistinguishable from each other in all of the 20 characters listed in the diagnosis, indicating that †*Phareoides* is a junior synonym of †*Phareodus*.

3. The Australian †*Phareodus queenslandicus* is phylogenetically most closely related to †*P. encaustus* from North America. This relationship is mainly supported by the frontal consisting of a narrow posterior portion and a greatly expanded anterior portion, the hyomandibular bearing a long stick-like opercular process and a subtriangular anterior wing, the number of the dentary teeth, the preopercle with an indistinct horizontal arm, and the pattern of the posterior infraorbitals.

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APPENDIX 2-I: Measurements of †*Phareodus encaustus.*

	TL	FL	SL	BD	HL	HD	PPL	PVL	PDL	PAL	DFBL	AFBL	CPL	CPD
AMNH 4587	569	555	503	227	165	161	133	265	353	355	89	114	55	65
FMNH PF10256	?	545	485	210	144	121	116	236	345	315	101	119	65	56
FMNH PF10257	?	?	?	230	?	?	?	?	?	?	105	117	68	61
FMNH PF10285	520	410	453	195	145	120	127	236	327	308	80	110	57	57
FMNH PF10964	65	63	57	20	18	15	18	32	40	40	9	10	8	7
FMNH PF10965	49	47	42	15	13	13	13	23	29	29	6	8	6	5
FMNH PF10966	30	29	26	7	8	7	8	14	18	19	4	5	4	2.5
FMNH PF10967	82	79	71	25	22	19	22	37	50	49	11	14	12	5
FMNH PF11938	?	?	38	?	?	?	?	?	?	?	5	7	5	4
FMNH PF11944	600	570	507	230	170	140	125	247	355	330	100	125	60	61
FMNH PF11945	545	517	456	185	140	120	122	228	317	297	93	105	90	55
FMNH PF12408	49	47	42	12	15	12	15	24	29	29	5	6	7	3
FMNH PF12515	?	?	?	?	153	130	?	?	?	?	?	?	?	?
FMNH PF12681	542	509	449	210	147	130	135	230	315	274	92	110	76	58
FMNH PF12683	?	550	493	190	150	?	?	?	345	?	?	?	65	50
FMNH PF12685	?	?	?	190	?	?	?	?	?	?	93	117	66	58
FMNH PF13103	22	21.5	20	?	6	?	7	?	14	14	?	?	3	2
FMNH PF14040	650	597	540	232	165	160	147	280	400	345	108	118	75	66
FMNH PF14062	143	138	118	55	35	31	32	54	87	80	21	27	18	14
FMNH PF14063	223	215	191	76	45	50	49	95	132	131	34	42	28	20

APPENDIX 2-II: Measurements of †*Phareodus testis.*

	TL	FL	SL	BD	HL	HD	PPL	PVL	PDL	PAL	DFBL	AFBL	CPL	CPD
AMNH 743	160	156	135	61	38	42	40	73	95	94	23	30	19	11
AMNH 805	?	192	170	87	50	50	51	85	118	115	34	43	21	18
AMNH 1336	341	334	291	142	83	76	68	142	207	190	55	78	37	32
AMNH 2471	?	?	90	36	28	25	25	46	64	58	16	19	12	11
AMNH 2799	278	267	222	92	66	55	?	120	156	154	43	58	31	26
AMNH 5821	159	149	136	60	39	36	40	64	99	91	24	34	27	15
AMNH 6301	137	128	115	42	36	29	39	57	77	76	20	27	16	11
AMNH 11547	200	193	174	79	48	45	44	87	126	121	30	45	22	20
FMNH PF10627	162	148	130	61	41	35	37	61	91	82	24	34	19	16
FMNH PF10960	59	57	50	18	16	15	16	27	36	35	8	11	7	6
FMNH PF10969	72	69	60	23	17	13	18	30	42	40	11	14	9	6
FMNH PF11939	?	?	61	25	20	19	18	31	44	40	11	14	8	8
FMNH PF11942	350	333	295	120	71	66	81	163	209	194	54	72	37	29
FMNH PF11943	162	153	136	61	40	34	37	66	96	90	24	32	20	15
FMNH PF12409	132	125	112	45	33	31	30	55	81	76	16	25	20	13
FMNH PF12411	79	70	46	69	43	40	37	72	106	100	27	40	17	17
FMNH PF12412	?	153	133	54	40	29	39	65	95	87	24	33	16	15
FMNH PF12682	340	330	290	145	73	65	61	?	202	188	57	80	35	32
FMNH PF13035	153	144	125	55	36	32	34	61	88	83	22	32	17	19
FMNH PF13576	45	48	39	12	12	11	12	21	28	27	6	8	6	4
FMNH PF25014	260	242	215	97	60	53	58	107	145	140	41	55	30	24
FMNH PF26407	305	294	260	120	70	67	60	122	183	161	50	69	34	29
ROM 28560	177		144		43	40	40	74	103	97			29	14
UF 31	?	?	288	130	83	72	72	132	201	189	53	73	38	33
UALVP 447	205	190	166	76	50	51	43	81	121	108	31	44	20	19
UALVP 17657	?	?	166	73	50	51	43	78	113	104	34	48	21	19
UALVP 17658	371	340	304	134	100	101	75	144	212	199	59	82	39	32
UALVP 17659	187	176	155	70	47	44	45	78	109	104	30	39	21	18

Chapter 3

A LATE CRETACEOUS OSTEOGLOSSID FROM THE OLDMAN FORMATION OF ALBERTA, CANADA, AND ITS PHYLOGENETIC RELATIONSHIPS*

INTRODUCTION

Freshwater teleosts of Early Cretaceous through middle Paleocene age in North America are extremely important to studies of the evolution of the North American fish fauna because this was apparently a time of major biotic transition (Grande, 1986; Grande and Cavender, 1991). However, materials found so far from North American Cretaceous freshwater deposits are still far from sufficient to clarify the origins of the Cenozoic fish fauna of North America. Schaeffer (1949) named a freshwater teleost †*Ostariostoma wilseyi* on the only specimen collected from the Livingston Formation of Montana (Fig. 1). That species may be either Late Cretaceous or Paleocene in age (Schaeffer, 1949; Grande and Cavender, 1991). The first undoubted Cretaceous freshwater teleost from North America is †*Chandlerichthys strickeri* Grande, 1986, from the Albian or Cenomanian Chandler Formation of northern Alaska (Fig. 3-1). Both †*Ostariostoma* and †*Chandlerichthys* have been tentatively referred to Osteoglossomorpha (Grande, 1986; Grande and Cavender, 1991). Wilson et al. (1992) recently described two esocoid species (†*Oldmanesox canadensis* and †*Estesesox foxi*) based on fragmentary remains from the Upper Cretaceous of western North America.

In contrast to the rarity in the Cretaceous, teleosts have been found to be the dominant elements making up several well-documented late Paleocene freshwater fish faunas in North America. These late Paleocene teleosts have been referred to mostly

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*A version of this chapter is in press. Li Guo-qing, 1994: A Late Cretaceous osteoglossid (Teleostei) from the Oldman Formation of Alberta, Canada, and its phylogenetic relationships; pp.000-000 *in:* Arratia, G. and G. Viohl (eds.): Mesozoic Fishes-Systematics and Paleoecology. Proceedings of International Meeting, Eichstätt 1993; München (Dr. Pfeil), Germany.

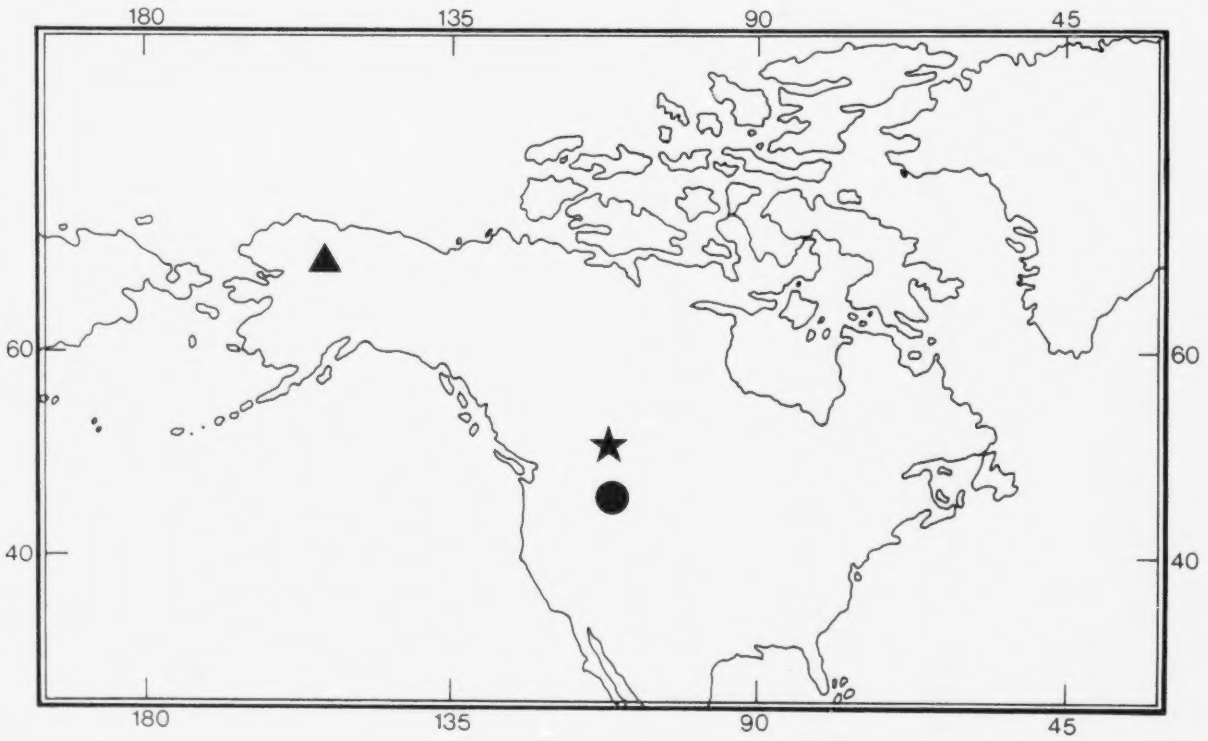

FIGURE 3-1: Map showing localities of the three North American Late Cretaceous teleosts referred to Osteoglossomorpha. Star stands for Steveville, the type locality of †*Cretophareodus* gen. nov., about 10km southwest of Wardlow, southeastern Alberta, Canada. Triangle stands for the type locality of †*Chandlerichthys* in Arctic Slope of northern Alaska, USA; and the circle for Raw Liver Creek, the type locality of †*Ostariostoma* in Madison Range, Montana, USA.

extinct genera within extant taxa such as Ictaluridae (Lundberg, 1975), Osteoglossomorpha, Gonorynchidae, Cyprinoidea, Esocidae, Percopsidae (Wilson, 1980), or Paracanthopterygii (Grande, 1988), the extinct family Asineopidae, and Osmeridae, (Wilson and Williams, 1991, 1993).

Sternberg (1941) reported the discovery of "new teleosts from the Canadian Cretaceous" in an abstract submitted to the proceedings of the Royal Society of Canada, but the specimens were neither described nor properly named. I am fortunate to examine one of the specimens referred to by Sternberg. It was found in the Upper Cretaceous Oldman Formation of southern Alberta, Canada (Fig. 3-1). My study suggests that the specimen represents a new fossil osteoglossomorph that provides some new information about the phylogeny of the Eocene osteoglossid †*Phareodus*.

Geology

The Oldman Formation (Russell and Landes, 1940) of Campanian age represents an important part of the Late Cretaceous freshwater deposits in southern Alberta. It is both overlain and underlain by marine deposits, the Bearpaw Formation (Christiansen, 1967) and the Foremost Formation (Russell and Landes, 1940). Further investigation made by Russell (1964) indicates that the Oldman Formation (best exposed in Dinosaur Provincial Park) corresponds to the upper part of the Judith River Formation of Montana. Although it was suggested that use of the name be discontinued (Mclean, 1971, 1977), "Oldman Formation" has been retained by some paleontologists (e.g. Fox, 1979; Gao, 1992; Wilson et al., 1992), in consideration of its convenient use as a local lithological unit.

The age of the Oldman Formation has been estimated at 74.9 -78.2Ma based on radioisotopic and radiometric studies of bentonites in this formation (Thomas et al., 1990; Eberth, 1988, 1990, and 1992, pers. comm.; Eberth et al., 1990).

Vertebrate paleontological investigation, including microfossils, in the Oldman Formation has provided important information on fishes (Bardack, 1970; Dodson, 1983, 1987; Brinkman, 1990; Wilson et al., 1992).

Comparative Materials

Specimens studied for this chapter consist of fossil specimens, Recent dried skeletons, and preserved Recent specimens.

†Lycopteriformes– †*Lycoptera davidi* (Sauvage), specimens including those listed in Liu et al. (1963), Ma (1987), and AMNH FF19400, 19403. †*Tongxinichthys* *microdus* Ma, specimens listed in Ma (1980).

Hiodontiformes– Hiodontidae: *Hiodon tergisus* Lesueur and *Hiodon alosoides* (Rafinesque), specimens listed in Chapter 6.

Osteoglossiformes– Osteoglossidae: *Osteoglossum bicirrosum* (Vandelli), one alizarin prepared specimen (UAMZ 4642, SL = 177). *Osteoglossum ferreirai* Kanazawa, four alizarin prepared young specimens (UAMZ 6753-6754, SL ranging from 48 to 61). †*Phareodus testis* (Cope) and †*Phareodus encaustus* (Cope), specimens listed in Chapter 2. *Arapaima gigas* (Cuvier), one specimen (UAMZ 2244, SL=285). †*Sinoglossus lushanensis* Su, specimens listed in Su (1986).

Pantodontidae: *Pantodon buchholsi* Peters, three alcoholic preserved (UAMZ 2273, SL ranging from 60 to 67) and one alizarin prepared (UAMZ 6751, SL=72) specimens.

SYSTEMATIC PALEONTOLOGY

Subdivision Teleostei Müller, 1846
Superorder Osteoglossomorpha Greenwood et al., 1966
Order Osteoglossiformes Berg, 1940
Suborder Osteoglossoidei Berg, 1940
Family Osteoglossidae Bonaparte, 1850
Subfamily Osteoglossinae Bonaparte, 1850

Included Genera– †*Cretophareodus* gen. nov., †*Phareodus*, *Pantodon*, †*Singida*, *Osteoglossum*, and *Scleropages*.

Diagnosis– Osteoglossids differing from Heterotidinae in the following features: basihyal tooth plate fused with basibranchial tooth plate; jaw articulation behind vertical middle line of orbit; horizontal arm of preopercle short, ending anteriorly far behind orbit; preoperculo-mandibular canal opening in a groove on horizontal arm of preopercle; opercle subsemicircular; presence of fused palato-ectopterygoid; first pectoral fin ray particularly strong and long, with distal end extending to or beyond pelvic fin

Genus †*Cretophareodus* gen. nov.

Type Species– †*Cretophareodus alberticus* gen. et sp. nov.

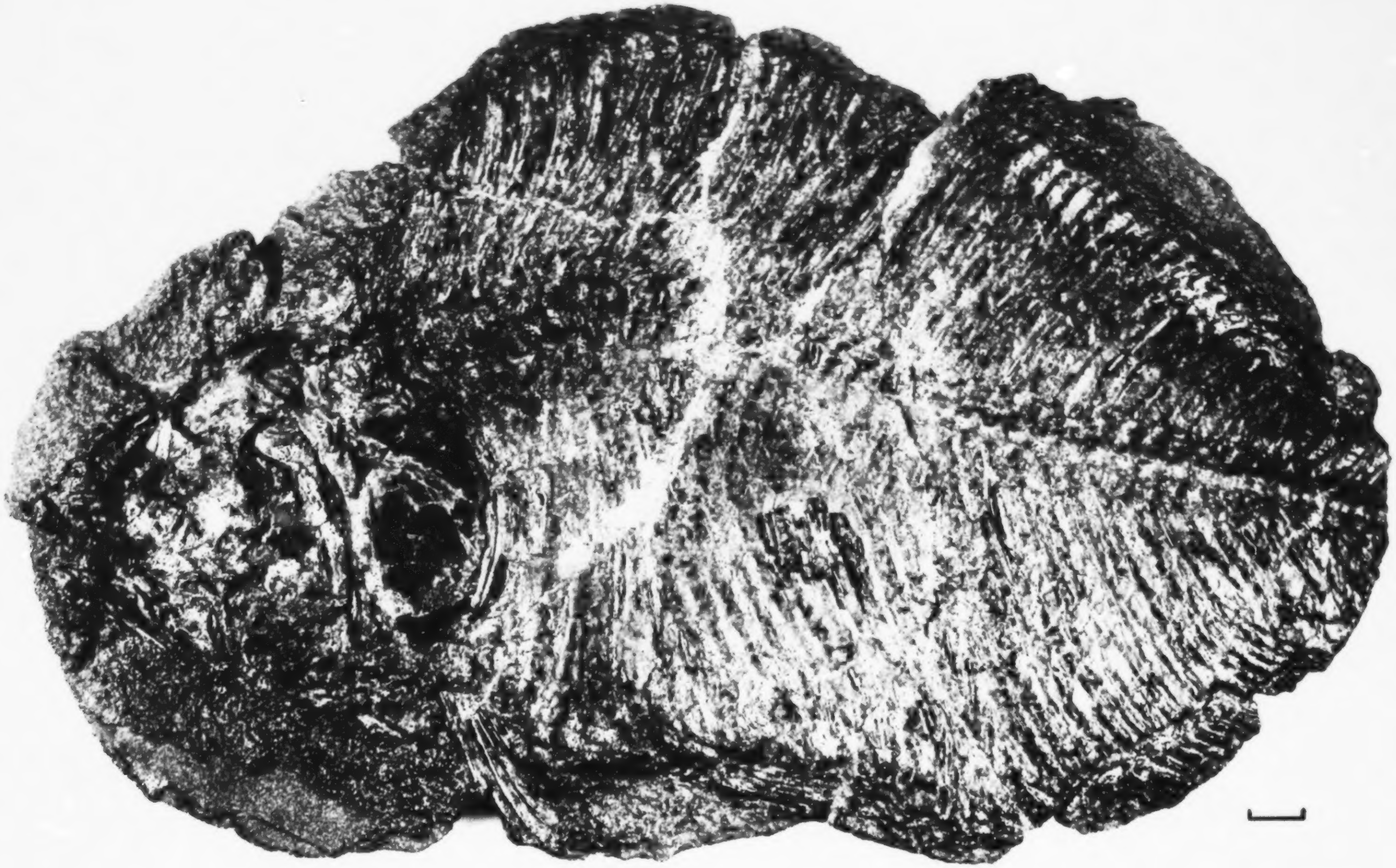

FIGURE 3-2: Holotype of †*Cretophareodus alberticus* gen. et sp. nov. (ROM 1323a). Scale bar equals 10mm.

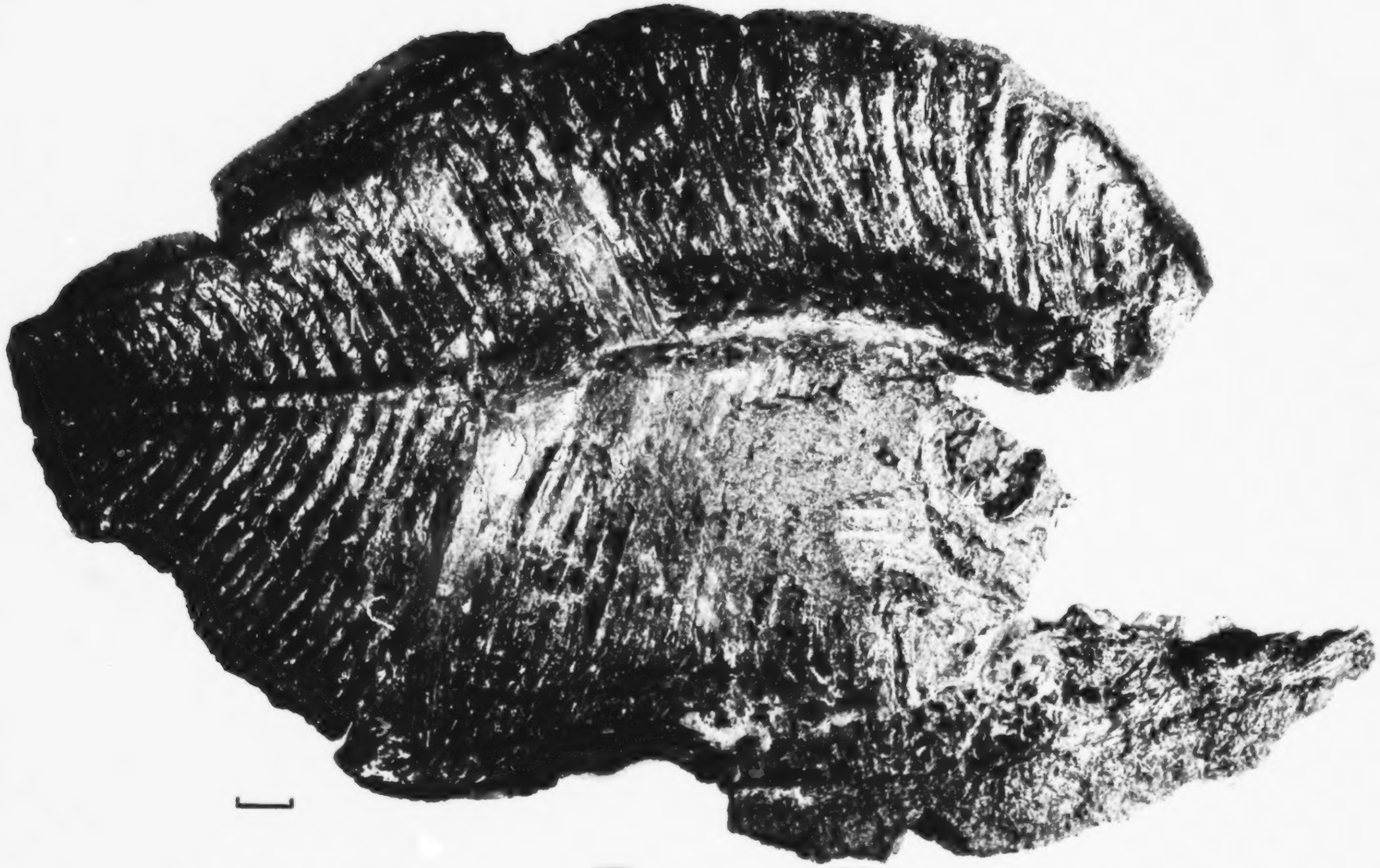

FIGURE 3-3: Holotype of †*Cretophareodus alberticus* gen. et sp. nov. (ROM 1323b). Scale bar equals 10mm.

Diagnosis– Osteoglossinae differing from all other genera in subfamily in having: corner of mouth cleft lying at level of posterior margin of orbit, articulation facet for quadrate on articular and retroarticular, six-rayed pectoral fin rays, dorsal fin larger than anal fin, anal fin origin opposite middle of dorsal fin, subcycloid scales with fine growth lines interrupted by both basal and apical radii, head depth to head length ratio about 0.78, depth to width of opercle ratio 1.72.

Etymology– The generic name is coined by combining "Creto-" for Cretaceous with "*Phareodus*," gender masculine.

†*Cretophareodus alberticus* gen. et sp. nov.

(Figs. 3-2 to 3-4)

Diagnosis– Same as that for the genus.

Holotype– ROM 1323, an incomplete fish in part and counterpart.

Etymology– The specific name honors the province in which the first specimen of this species was found.

Locality and Horizon– Steveville, Alberta (Fig. 3-1); Oldman Formation, Upper Cretaceous (middle Campanian).

Description

The part (ROM 1323a) exposed from left side is better preserved than the counterpart (ROM 1323b) in having a nearly complete outline of the head region.

Measurements of Holotype– BD=142, HL=~90, HD =~70, OD=43, OW=25, PPL=80, PVL=135, PAL=200, PDL=170, AFBL=55, DFBL=75.

Meristics of Holotype– BR=~7, PCV=23-25, PFR=6, VFR=5, AFR=~17, AP=17, DFR=~21, DP=21.

Neurocranium and Skull Roof– All of the dermal bones covering the skull roof are damaged. Judging from the impression on ROM 1323a, the supraoccipital does not separate the parietals. The parietal appears to be as broad as the posterior part of the frontal. Part of the right frontal preserved on the specimen suggests that it is at least 1.5 times as broad anteriorly as posteriorly (Fig. 3-4). The nasal is not preserved.

Opercular System– The right preopercle on ROM 1323a resembles that of †*Phareodus* in shape (Figs. 3-2, 3-4). This bone has a narrow vertical arm about two times as long as the horizontal arm. The upper part of the vertical arm is slightly pointed anteriorly; the horizontal arm is short with a distinct postero-ventral expansion. The two

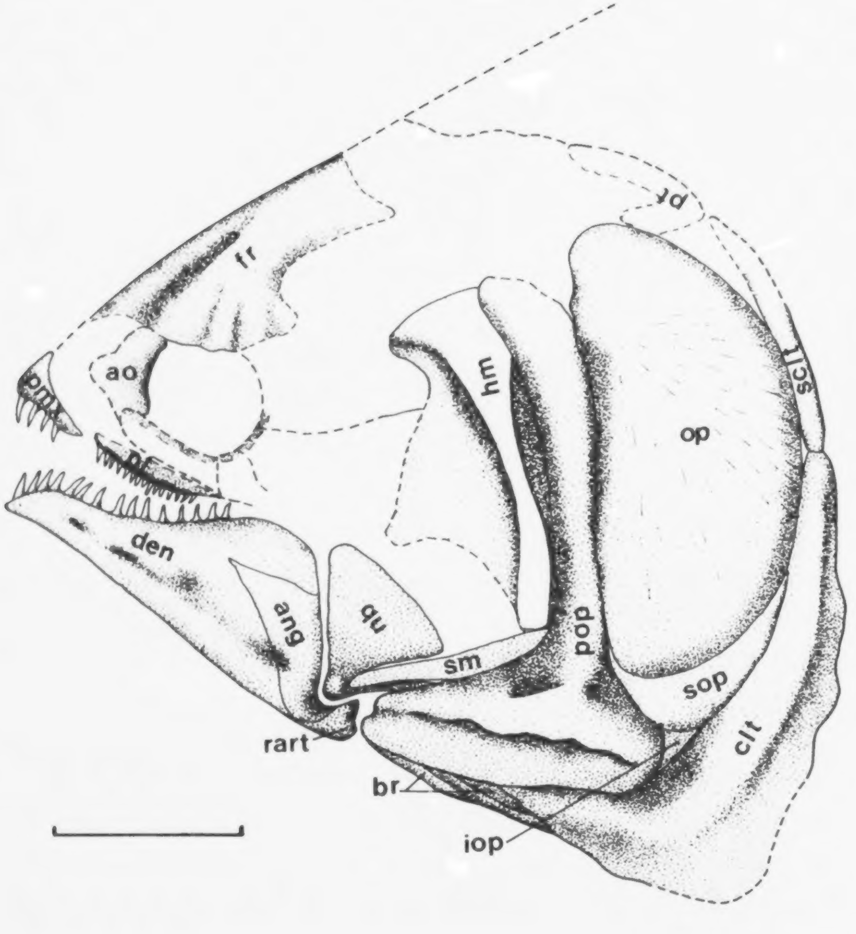
pt
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FIGURE 3-4: Partial restoration of the cranial skeleton of †*Cretophareodus alberticus* gen. et sp. nov., based on ROM 1323a. Scale bar equals 20mm.

arms of this bone form an approximate right angle. The preopercular canal runs near the anterior margin of the vertical arm, possibly opening in a groove on the horizontal arm.

The interior view of the right opercle exposed on ROM 1323a shows a subsemicircular outline (Figs. 3-2, 3-4). The lower 3/4 of the front edge of this bone is nearly straight. The width of the bone (the largest distance between the front edge and the posterior edge) is about 0.58 times its depth (the largest distance between the dorsal and ventral edges). As in the Eocene †*Phareodus* (Fig. 3-7), the external surface of this bone is radially sculptured.

The subopercle is subtriangular and resembles that of †*Phareodus* in shape.

Orbital Region– There are at least two broad infraorbitals behind the orbit; they may extend posteriorly to the front edge of the preopercle. It is, however, impossible to give a full description of the infraorbitals because of damage to this region.

Jaws and Palatopterygoid Arch– Sharp conical teeth are developed on both the lower and the upper jaws. The premaxilla and maxilla appear to be similar to those in †*Phareodus*. A supramaxilla is absent. The dentary is somewhat comparable to that in †*Phareodus testis*. It is shallow anteriorly and deep posteriorly. Teeth on this bone are arranged in at least two rows.

The angular is expanded posteriorly; it is not clear whether this dermal bone has fused with the articular or not. The articular is partly preserved on the specimen. A small retroarticular can be seen immediately behind the postero-ventral corner of the articular.

The quadrate and symplectic are similar to those in †*Phareodus* (e.g., UALVP 17658) in shape. The quadrate articulates with the articular by a strong head. A large articular facet is developed in the articular and the dorsal surface of the retroarticular.

Of the elements of the palatopterygoid arch, only the strongly toothed palatine is partly preserved.

Hyoid Arch– Only an incomplete impression of the hyomandibular is seen; it is vertically ridged and articulates with the cranium by a single head (Figs. 3-2, 3-4).

Parts of at least 7 slender branchiostegals are visible.

Vertebral Column– Although all but the first two or three vertebrae are missing, impressions are left on the specimen. The vertebral column is arched dorsally before the dorsal fin (Figs. 3-2, 3-3). Measurement of the impression of a single vertebra indicates that it is slightly higher than it is long. About 23-25 precaudal vertebrae can be counted on the basis of impressions of the ribs, neural spines, and vertebrae.

Epineurals are present on the precaudals, and extend postero-dorsally from the base of the corresponding neural arch.

About 16 slender and slightly curved supraneurals or their impressions can be seen on the specimen; they alternate with the neural spines of the predorsal vertebrae. Each supraneural has a distal end extending almost to the dorsal margin of the body.

The ribs have been destroyed, leaving only their slender impressions. Each rib is very long with a length approximately equal to 3/5 of the body depth, suggesting a very spacious abdominal cavity in this fish.

Elongated neural and haemal spines are strongly developed on the preserved caudal vertebrae.

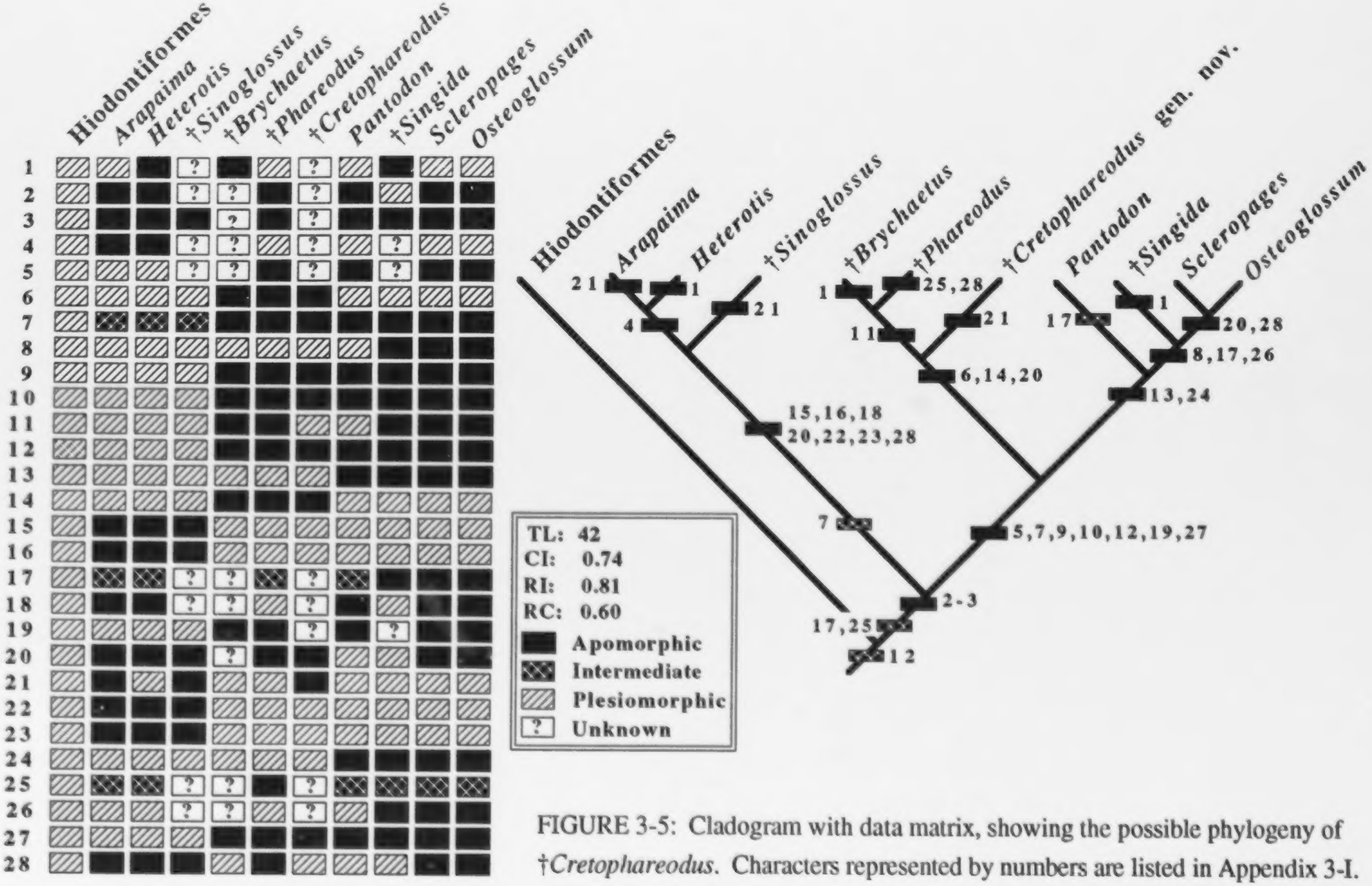
Pectoral Girdle and Fin– Only the right cleithrum (Figs. 3-2) is partly preserved on the specimen. It is a strong, sickle-shaped bone. About 6 pectoral fin rays are seen, the first ray being the strongest, according to the impression, and distally segmented; others are distally branched and segmented.

Pelvic Girdle and Fin– An impression of the support for the pelvic fin is shown on both ROM 1323a and 1323b. It is tapered and similar to that in other osteoglossids. The pelvic fins are ventrally situated and consist of five rays. The distance between the pelvic and the pectoral fins is almost equal to that between the pelvic fins and the anal fin.

Dorsal Fin and Anal Fin– A large dorsal fin is developed in this fish, consisting of at least 21 principal rays supported by 21 dorsal pterygiophores (ROM 1323a). The anteriormost dorsal pterygiophore inserts five to six vertebrae anterior to the anteriormost anal pterygiophore.

The anal fin is distinctly smaller than the dorsal fin with a base length as long as about 0.73 that of the dorsal fin. It originates opposite to the middle of the dorsal fin and consists of at least 17 principal rays supported by 17 anal pterygiophores (ROM1323a). The last anal fin ray is double.

Scales– This fish is covered by thin cycloid scales that are not reticulated. Each of the scales is broader than long and has a subbasal nucleus (scale focus). Both the basal and apical radii are present and arranged radially. The basal radii are more numerous than the apical radii, which are spaced slightly more widely. Scales along the lateral line are perforated. Depressions seen from the interior surface of the lateral line scales above the caudal vertebral centra on ROM 1323b are supposed to have contained neuromasts.



	Hiodontiformes	*Arapaima*	*Heterotis*	†*Sinoglossus*	†*Brychaetus*	†*Phareodus*	†*Cretophareodus*	*Pantodon*	†*Singida*	*Scleropages*	*Osteoglossum*
1	▨	▨	■	?	■	▨	?	▨	■	▨	▨
2	▨	■	■	?	?	■	?	■	▨	■	■
3	▨	■	■	■	?	■	?	■	■	■	■
4	▨	■	■	?	?	▨	?	▨	?	▨	▨
5	▨	▨	▨	?	?	■	?	■	?	■	■
6	▨	▨	▨	▨	■	■	■	▨	▨	▨	▨
7	▨	▩	▩	▩	■	■	■	■	■	■	■
8	▨	▨	▨	▨	▨	▨	▨	▨	■	■	■
9	▨	▨	▨	▨	■	■	■	■	■	■	■
10	▨	▨	▨	▨	■	■	■	■	■	■	■
11	▨	▨	▨	▨	■	■	▨	▨	■	■	■
12	▨	▨	▨	▨	■	■	■	■	■	■	■
13	▨	▨	▨	▨	▨	▨	▨	■	■	■	■
14	▨	▨	▨	▨	■	■	■	▨	▨	▨	▨
15	▨	■	■	■	▨	▨	▨	▨	▨	▨	▨
16	▨	■	■	■	▨	▨	▨	▨	▨	▨	▨
17	▨	▩	▩	?	?	▩	?	▩	■	■	■
18	▨	■	■	?	?	▨	?	■	▨	■	■
19	▨	▨	▨	▨	■	■	?	■	?	■	■
20	▨	■	■	■	?	■	■	▨	▨	■	■
21	▨	■	▨	■	▨	▨	■	▨	▨	▨	▨
22	▨	■	■	■	▨	▨	▨	▨	▨	▨	▨
23	▨	■	■	■	▨	▨	▨	▨	▨	▨	▨
24	▨	▨	▨	▨	▨	▨	▨	■	■	■	■
25	▨	▩	▩	?	?	■	?	▩	▩	▩	▩
26	▨	▨	▨	?	?	▨	?	▨	■	■	■
27	▨	▨	▨	▨	■	■	■	■	■	■	■
28	▨	■	■	■	▨	■	▨	▨	▨	■	■

Hiodontiformes
Arapaima
Heterotis
†Sinoglossus
†Brychaetus
†Phareodus
†Cretophareodus gen. nov.
Pantodon
†Singida
Scleropages
Osteoglossum
21
1
4
21
15,16,18
20,22,23,28
7
1
25,28
11
21
6,14,20
17
1
20,28
8,17,26
13,24
5,7,9,10,12,19,27
2-3
17,25
12
TL: 42
CI: 0.74
RI: 0.81
RC: 0.60
■ Apomorphic
▩ Intermediate
▨ Plesiomorphic
? Unknown

FIGURE 3-5: Cladogram with data matrix, showing the possible phylogeny of †*Cretophareodus*. Characters represented by numbers are listed in Appendix 3-I.

DISCUSSION

Because of the poor preservation of the only specimen and the absence of most characters from the specimen, it is very difficult to carry out a satisfactory discussion of the phylogeny of †*Cretophareodus* gen. nov.

In general, it is easy to distinguish †*Cretophareodus* gen. nov. from all of the known genera in Osteoglossomorpha. Although I can define only two autapomorphies for this new genus at present, the pectoral fin consisting of only 6 rays and the depth to width of the opercle ratio 1.72, it is also characterized by the following combination of characters: a dorsal fin that is larger than the anal fin and beginning much in advance of the anal fin, pelvic fins half-way between the anal and the pectoral fins, and fine growth lines on the subcycloid scales being interrupted by both the anterior (basal) and the posterior (apical) radii.

A general comparison with known osteoglossiform fishes both fossil and Recent is made, with the assistance of a cladistic analysis of 28 skeletal characters, which are all observable on the fossil specimens (see Appendix 3-I). All characters were initially assumed to be unordered. The polarity of the characters was determined by comparison with the condition in the presumed osteoglossiform sister-group Hiodontiformes. This comparison suggests that †*Cretophareodus* gen. nov. is one of the genera in Osteoglossidae, especially closely related to the members in the clade of Osteoglossinae (Fig. 3-5). The following characters, which are considered to be the synapomorphies of Osteoglossinae in this thesis, may support the relationship.

1. Subsemicircular opercle: In osteoglossomorph fishes, four basic types of opercle may be identified (Fig. 3-6). In some primitive osteoglossomorphs such as †*Lycoptera* Müller (1847), the opercle is kidney-shaped (Fig. 3-6A). Hiodontidae possess a subrectangular opercle that may have a protruding upper posterior border and an acute postero-dorsal projection (e.g., *Hiodon*) (Fig. 3-6B) (also see Chapter 6).

The opercle in Osteoglossidae may be either subsemicircular like that seen in *Osteoglossum* (Fig. 3-6C), or oval as in *Arapaima* (Fig. 3-6D). These two types of opercle divide the family Osteoglossidae into two groups, one with a subsemicircular opercle, represented by *Osteoglossum* and *Scleropages*, and the other with an oval opercle, represented by *Arapaima* and *Heterotis*, in which the posterior edge of the opercle may be serrated.

In the known fossil osteoglossomorph fishes, a subsemicircular opercle has so far been seen in †*Phareodus* Leidy, 1873 (Fig. 3-7), †*Brychaetus* Woodward, 1901 (see

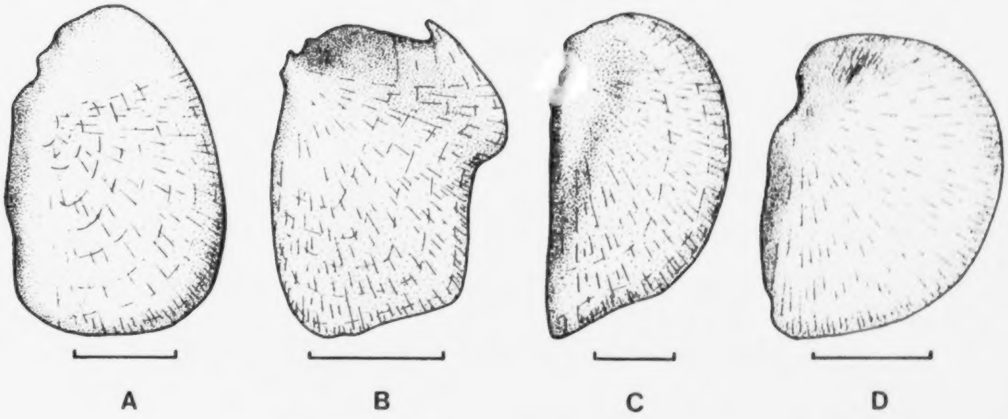


FIGURE 3-6: Four basic patterns of the opercle in Osteoglossomorpha. **A**, †*Lycoptera davidi*, based on AMNH FF19403. **B**, *Hiodon alosoides*, drawn from UAMZ 6714. **C**, *Osteoglossum bicirrosum*, from UAMZ 4642. **D**, *Arapaima gigas*, from UAMZ 2244. Scale bar for **A** equals 2mm, for **B** and **D** 10mm, and for **C** 5mm.

Roellig, 1974; Taverne, 1973, 1974), †*Singida* (Fig. 3-8) and †*Musperia* Sanders, 1934 (possibly synonymous with †*Phareodus*). The opercle in †*Cretophareodus* gen. nov. (Fig. 3-2 and 3-4) is almost identical to that of †*Phareodus*, which has a relatively straight anterior edge and a rounded posterior edge. This character is considered to be one of the most important synapomorphies shared by all of the genera in Osteoglossinae

2. A short horizontal arm of preopercle extending anteriorly only to the level of the postero-ventral corner of the 3rd infraorbital: The horizontal arm of the preopercle shows two basic conditions in osteoglossomorphs. In most taxa including Hiodontidae, Notopteridae, and fossil †*Sinoglossus* (Su, 1986), the anterior end of the horizontal arm of the preopercle extends anteriorly to the level of the posterior edge of the orbit, or it may reach to the anterior 1/2 of the second infraorbital (e.g., *Heterotis*, Ridewood, 1905; Kershaw, 1976; Taverne, 1977). The horizontal arm of the preopercle in *Arapaima* seems not as long as that in *Heterotis*; it extends, however, to the anterior half of the third infraorbital. In contrast to this condition, the horizontal arm of the preopercle in *Osteoglossum*, *Scleropages*, and *Pantodon* is very short; it extends anteriorly only to the level of the postero-ventral corner of the third infraorbital. †*Phareodus* (Fig. 3-7) and †*Brychaetus* have a preopercle that resembles that in *Osteoglossum* and *Scleropages*. The horizontal arm in †*Singida* is unusual among osteoglossomorphs in having a long triangular posterior projection; its anterior end reaches also only to the level of the postero-ventral corner of the io3 (Fig. 3-8). The preopercle in †*Cretophareodus* gen. nov. is almost indistinguishable from that in †*Phareodus*. This may be additional evidence linking †*Cretophareodus* with the subfamily Osteoglossinae.

3. The preoperculo-mandibular canal on the horizontal arm of the preopercle opening in a groove: The preoperculo-mandibular canal on the horizontal arm of the preopercle opens in a groove in the Recent *Osteoglossum* and *Scleropages*. A similar condition is also present in the fossil †*Phareodus* (Fig. 6-7), †*Brychaetus*, and †*Singida*. Judging from the impression of the preopercle on the only specimen, the preoperculo-mandibular canal on the horizontal arm of the preopercle of †*Cretophareodus* gen. nov. also opens in a groove similar to that in †*Phareodus* and *Osteoglossum*. This important character state makes the genera in Osteoglossinae distinct from all other members of Osteoglossomorpha.

4. Jaw articulation posteriorly located: Among the Recent osteoglossids, *Heterotis* and *Arapaima* have a shallow gape (mouth cleft) with the angle of the jaws located anterior to the orbit. The same condition is present in †*Sinoglossus* and the

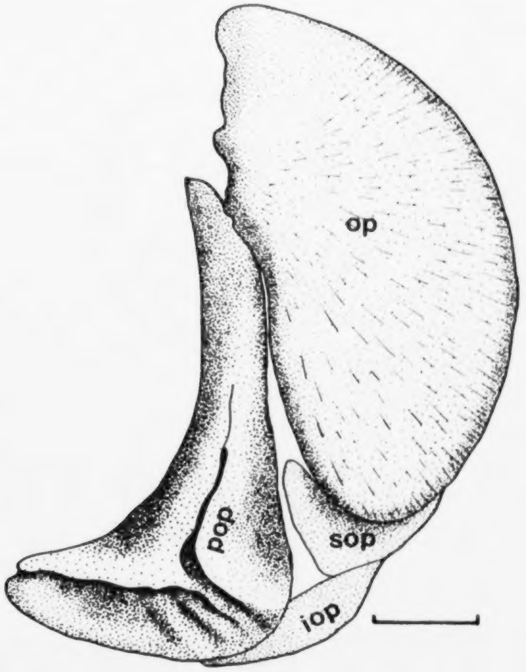

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FIGURE 3-7: Opercular series of †*Phareodus testis*, drawn from FMNH PF12682. Scale bar equals 10mm.

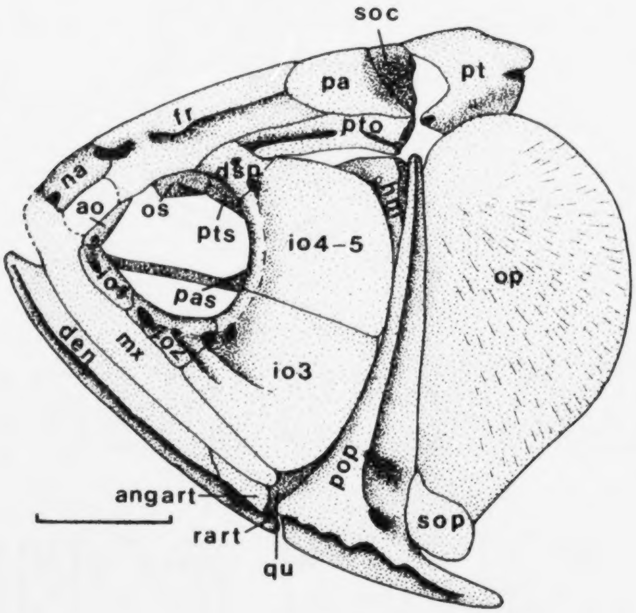
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FIGURE 3-8: Restoration of the cranial skeleton of †*Singida jacksonoidees*, modified from Greenwood and Patterson (1967). Scale bar equals 10mm.

primitive teleosts †*Pholidophorus* and †*Leptolepis* (Patterson, 1967, 1975). In *Hiodon*, the angle of the jaws may be located behind the anterior edge of the orbit, but it does not extend posteriorly to beyond the posterior end of the first infraorbital.

In contrast, a deep gape is present in the Recent *Osteoglossum* and *Scleropages*, with the angle of the jaws far behind the orbit. A similar condition may be imagined in †*Singida* if the jaws were opened to their maximum extent (Fig. 3-8) (according the plates and text-figures in Greenwood and Patterson, 1967). The gape in †*Phareodus* (see Figs. 2-3 and 2-9) and †*Brychaetus* is slightly shallower than that in *Osteoglossum* and *Scleropages*; however, the corner of the gape is still much more posteriorly located than in Heterotidinae, extending posteriorly to beyond the level of the second infraorbital. The corner of the mouth cleft in †*Cretophareodus* gen. nov. is located at the level of the posterior edge of the orbit (Figs. 3-2 and 3-4). A relatively deep mouth cleft with the angle of the jaws posteriorly located could thus be another important character state linking †*Cretophareodus* gen. nov. to Osteoglossinae.

5. First pectoral fin ray strong and long: Among the previously known Osteoglossidae, an enlarged first pectoral ray that may extend to or beyond the pelvic fin is seen in the Recent *Osteoglossum*, *Scleropages*, and in the Eocene †*Phareodus*. This character is also present in †*Brychaetus* and in †*Singida*, which is considered to be a member of Osteoglossinae in this thesis. The first pectoral fin ray in †*Cretophareodus* gen. nov. is similar to that in other genera of Osteoglossinae.

Although I can not reliably determine to which of the genera in Osteoglossinae †*Cretophareodus* gen. nov. is most closely related, two synapomorphies (characters 6 and 14 in Appendix 3-I) and one other character state (23-25 precaudal vertebrae) suggest that this new genus may be the sister-group of †*Phareodus* and †*Brychaetus*. These three genera are together the "stem-group" (Jefferies, 1979; Wilson, 1992) of the Osteoglossinae. Considering the opercular series and the position of the jaw articulation, †*Cretophareodus* gen. nov. seems to be more closely related to †*Phareodus testis* (Fig. 3-7). This relationship, however, needs to be clarified by study of better preserved material.

It is noticeable that the vertebral column of †*Cretophareodus* gen. nov. is similar to that in †*Chandlerichthys*, which was supposed to be a primitive osteoglossomorph (Grande, 1986). In that genus the vertebral column is also dorsally arched before the dorsal fin and downturned anteriorly. Grande supposed that this kind of downturned anterior curvature of the vertebral column might be pathological. If Grande is correct, this feature may not be an important similarity between †*Cretophareodus* gen. nov. and

†*Chandlerichthys*. The laterally-compressed deep body is also seen in †*Chandlerichthys*. However, the poor preservation of the specimens referred to †*Chandlerichthys* makes it difficult to carry out a further investigation of that genus.

Previously, fossil osteoglossids had been mainly found in the Eocene deposits. †*Cretophareodus* gen. nov. is, however, the oldest undoubted member of the Osteoglossinae found so far. This new genus and species is considered to be an important link for the North American freshwater teleost fauna between the Jurassic and the Paleocene times.

CONCLUSIONS

†*Cretophareodus* gen. nov. is an early member of the subfamily Osteoglossinae. The subsemicircular opercle, horizontal arm of the preopercle, position of the jaw articulation (angle of the mouth), open canal on the horizontal arm of the preopercle, and large first pectoral fin ray closely link this new genus to †*Phareodus*, †*Brychaetus*, †*Singida*, *Osteoglossum*, and *Scleropages* in a monophyletic group.

†*Cretophareodus* gen. nov. may be the sister-genus of †*Phareodus* plus †*Brychaetus*. This relationship is supported by the frontal being at least 1.5 times anteriorly as broad as posteriorly, the laterally-compressed deep body with a large abdominal cavity, and the number of precaudal vertebrae.

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APPENDIX 3-I

28 characters used in cladistic analysis

1. Teeth on parasphenoid: (TP)
   [0] = present
   [1] = absent

2. Uroneurals: (Un)
   [0] = present
   [1] = absent

3. Principal caudal fin rays: (Pcfr)
   [0] = eighteen or more
   [1] = seventeen or fewer

4. Tooth plate on basihyal: (Tpb)
   [0] = present
   [1] = absent

5. Basihyal tooth plate and basibranchial tooth plate: (Bhbb)
   [0] = separate from each other
   [1] = fused with each other

6. Body shape: (BS)
   [0] = fusiform
   [1] = oval or deep with a large abdominal cavity

7. Opercle: (Op)
   [0] = irregular parallelogram
   [1] = oval or somewhat kidney-shaped
   [2] = subsemicircular

8. postero-ventral margin of opercle: (Pmop)
   [0] = rounded
   [1] = distinctly concave

9. Horizontal arm of preopercle: (Hap)
   [0] = extending anteriorly to beneath orbit
   [1] = extending anteriorly behind the orbit

10. Branches of preoperculo-mandibular canal on horizontal arm of preopercle: (Pomc)
    [0] = distributed as separate openings
    [1] = connected with each other to form a horizontal groove

11. Hyomandibular: (Hm)
    [0] = anterior not much expanded
    [1] = with a greatly expanded subtriangular anterior wing

12. Jaw articulation (angle of jaws): (JA)
    [0] = anterior to or beneath the orbit
    [1] = behind the orbit

13. Direction of mouth cleft: (Dmc)
    [0] = anteriorly directed
    [1] = strongly upturned

14. Frontal: (Fr)
    [0] = anteriorly narrower or only slightly broader than posteriorly
    [1] = anterior portion about twice as broad as posterior portion

15. Antorbital and the first infraorbital: (Aio1)
    [0] = separate from each other
    [1] = fused with each other

16. The second infraorbital: (Io2)
    [0] = small and slender
    [1] = large and irregularly wide trapezoidal in shape

17. Number of hypurals: (#H)
    [0] = seven or more
    [1] = six
    [2] = five or fewer

18. Upper hypurals and the second ural: (Uhu2)
    [0] = not fused
    [1] = fused

19. Posterior edge of the nasal: (Nape)
    [0] = straight or slightly curved
    [1] = strongly curved and extending backward

20. Shape of dorsal fin: (SDF)
    [0] = triangular
    [1] = rounded

21. Anal fin: (AF)
    [0] = larger than dorsal fin
    [1] = smaller than or as large as dorsal fin

22. "Cheek wall" formed by enlargement of 1st to 3rd infraorbitals: (CKW)
    [0] = absent
    [1] = present

23. Posterior end of maxilla: (Pemx)
    [0] = lying on angular
    [1] = lying on dentary part

24. Postero-ventral corner of preopercle: (Popc)
    [0] = rounded
    [1] = angulate

25. Neural spine on u1: (Nu1)
    [0] = absent or rudimentary
    [1] = one complete
    [2] = double

26. Number of neural spines on pu1 (if present): (Npu1)
    [0] = one
    [1] = double

27. First pectoral fin ray: (Pfr1)
    [0] = normal
    [1] = strong and extremely long

28. Scales: (Sc)
    [0] = not reticulate
    [1] = reticulate

Chapter 4

THE DISCOVERY OF HETEROTIDINAE (OSTEOGLOSSIDAE) FROM THE PALEOCENE PASKAPOO FORMATION OF ALBERTA, CANADA

INTRODUCTION

When Wilson (1980) reported the first Paleocene teleostean fish fauna from western Canada, his materials were mainly collected from the Paskapoo Formation of Alberta. In total, seven teleost families were recognized, of which Osteoglossidae were represented by isolated dentaries, maxillae, premaxillae, and opercles that were referred to as the subfamily Heterotidinae. This has been changed since the "mass-death layer" was discovered in the Paskapoo Formation at the Joffre Bridge road cut in 1984 (Wilson and Williams, 1991).

Although Wilson did not give detailed description of those isolated bones referred to Heterotidinae, his identification has been confirmed by the discovery of three articulated specimens from the Paskapoo Formation at the Joffre Bridge locality (see the description in this chapter).

Wilson (1980) first noticed the importance of the Paleocene gap to the study of North American fish evolution. Grande (1986) and Grande and Cavender (1991) stressed that the fresh water teleosts from Cretaceous to Paleocene deposits are extremely important to studies of the evolution of the North American fish fauna. Recently this Cretaceous-Paleocene evolutionary gap of the North American fresh water fish fauna has been partly bridged by the discoveries of †*Esox tiemani* from the Paleocene of Alberta (Wilson, 1980), †*Chandlerichthys* (Osteoglossomorpha) from the lower Upper Cretaceous of Alaska (Grande, 1986), †*McConichthys* (Paracanthopterygii) from the lower Paleocene of Montana (Grande, 1988), †*Speirsaenigma* (Euteleostei) from the Paleocene of Alberta (Wilson and Williams, 1991), †*Estesesox* and †*Oldmanesox* (Esocoidei) from the Upper Cretaceous of Alberta, Montana, and Wyoming (Wilson et al., 1992), †*Cretophareodus* gen. nov. (Osteoglossomorpha) from the Upper Cretaceous of Alberta (see Chapter 3), as well as Schaeffer's (1949)

†*Ostariostoma* (Osteoglossomorpha) from the Upper Cretaceous or Paleocene of Montana (Grande and Cavender, 1991).

The main purposes of this chapter are: **1)** to describe a new genus of Heterotidinae (Osteoglossidae) based on three articulated specimens and 25 isolated bones; **2)** to discuss the phylogeny of Heterotidinae.

Geology

Paskapoo, as the name of a lithological unit, was originally identified and described as a "series" (Selwyn, 1874; Tyrrell, 1887) or as the "Paskapoo beds," representing the Paleocene freshwater deposits overlying the Upper Cretaceous dinosaur-bearing "Edmonton Series," distributed mainly in central Alberta. Allan and Sanderson (1945) later defined it as a "formation." Since then the name "Paskapoo Formation" has been commonly used (Russell and Singh, 1978; Lerbekmo et al.,1979; Russell, 1983, 1987; Wilson, 1978b, 1980; Fox, 1984a-b, 1990a-b, 1991a-b; Lerbekmo and Coulter, 1985; Wighton and Wilson, 1986; McLean, 1990; Demchuk and Hills, 1991; Pigg and Stockey, 1991; Fox et al., 1992; Lerbekmo et al., 1992; Naylor and Fox, 1993).

According to Demchuk and Hills (1991), the Paskapoo Formation can be subdivided into three members, in ascending order the Haynes Member, the Lacombe Member, and the Dalehurst Member. The road cut exposure at Joffre Bridge corresponds to the lower part of the Lacombe Member in the Paskapoo Formation. Wilson and Williams (1991) divided the road cut exposure at Joffre Bridge into 8 layers, of which layers 3 and 5 yield isolated fish bones, and layer 7 is called the "fish layer" from which numerous fossil fish specimens have been collected.

The age of the Paskapoo Formation at the Joffre Bridge locality is probably middle Tiffanian (Ti3) to possibly late Tiffanian (Ti4) based on the study of fossil mammals (Krause, 1978; Fox, 1984a-b, 1990a-b, 1991a-b). This age is confirmed by Demchuk (1990) on the study of palynology and by Lerbekmo et al. (1992) on megnetostratigraphy.

Besides fishes (Russell, 1928; Wilson, 1980; Wilson and Williams, 1991) and mammals, paleontological study of the Paskapoo Formation has also contributed to knowledge regarding amphibians (Naylor and Fox, 1993), mammal-like reptiles (Fox et al., 1992), mollusks (Tozer, 1956), insects (Wilson, 1978b; Wighton, 1980, 1982; Baker and Wighton, 1984; Wighton and Wilson, 1986), plants (Bell, 1949; Christophel, 1976; Taylor and Stockey, 1984; Crane and Stockey, 1985; Pigg and Stockey, 1991), and palynomorphs (Snead, 1969; Demchuk, 1987, 1990).

Comparative Materials

Osteoglossiformes– Osteoglossidae: *Osteoglossum bicirrosum* (Vandelli), one alizarin prepared specimen (UAMZ 4642, SL=177). *Osteoglossum ferreirai* Kanazawa, four alizarin prepared young specimens (UAMZ 6753-6754, SL ranging from 48 to 61). †*Cretophareodus alberticus* gen. et sp. nov. specimen examined in Chapter 3. †*Phareodus testis* (Cope) and †*Phareodus encaustus* (Cope), specimens examined in Chapter 2. †*Phareodus queenslandicus* Hills, casts of specimens listed in Hills (1934); *Arapaima gigas* (Cuvier), one specimen (UAMZ 2244, SL=285). †*Sinoglossus lushanensis* Su, specimens listed in Su (1986).

Pantodontidae: *Pantodon buchholsi* Peters, one alizarin prepared specimen (UAMZ 6751, SL=72; three specimens preserved in alcohol (UAMZ 2273, SL=60-67).

Notopteridae: *Notopterus chitali* (Hamilton), four alizarin prepared specimens (UAMZ 6756, SL ranging from 72 to 82). *Xenomystus nigri* (Günther), two complete alizarin prepared specimens (UAMZ 2272, SL=132; UAMZ 6752, SL=125).

Osteoglossomorpha incertae sedis– †*Huashia* Chang and Chou, specimens listed in Chang and Chou (1977) and Ma (1986). †*Kuntulunia* Liu et al., specimens listed in Liu et al. (1982, 1985) and Zhang (1990).

SYSTEMATIC PALEONTOLOGY

Subdivision Teleostei Müller, 1846
Superorder Osteoglossomorpha Greenwood et al., 1966
Order Osteoglossiformes Berg, 1940
Suborder Osteoglossoidei Berg, 1940
Family Osteoglossidae Bonaparte, 1850
Subfamily Heterotidinae Bonaparte, 1850

Included Genera– †*Joffrichthys* gen. nov., †*Sinoglossus, Heterotis*, and *Arapaima*.

Emended Diagnosis– Osteoglossids differing from Osteoglossinae in the following features: opercle oval, io2 large and broadly trapezoidal, posterior end of maxilla lying on dentary, horizontal arm of preopercle about as long as vertical arm and extending to anterior 1/3 of orbit, preoperculo-mandibular canal giving off three branches on horizontal arm of preopercle, jaw articulation (angle of jaws) anterior to orbit, pelvic fin small and closer to anal fin than to pectoral fins.

Genus †*Joffrichthys* gen. nov.

Diagnosis– Paleocene Heterotidinae differing from Recent genera in having small pectoral fins, both dorsal and anal fins consisting of the same number of principal rays, caudal vertebrae "H"-shaped, scales cycloid with nearly central foci but no reticulation, 18 pairs of ribs, supraneurals 18, BR 8, PFR 10-12 (total), VFR 6(total), DFR 24 (total), DP 24, AFR 24 (total), AP 25, TV 48-51 (22 PCV + 26-29 CV).

Etymology– This new genus is named for the Joffre Bridge locality, at which the holotype specimen was discovered

Type Species– †*Joffrichthys symmetropterus* gen. et sp. nov.

†*Joffrichthys symmetropterus* gen. et sp. nov.

(Figs. 4-1 to 4-5)

Diagnosis– Same as that for the genus. Measurements as percentage of SL: HL/SL= 28%, HD/SL=33%, BD/SL=51%, PDL/SL=62%, PAL/SL=58%, PPL/SL=32%, CPL/SL=12%, DFBL/SL=32%, and AFBL/SL=36%.

Holotype– UALVP 23705a-b, a nearly complete individual (part and counterpart) (Fig. 4-1), SL=90, collected by Mr. Luke Allan Lindoe in 1986 from the "fish layer."

Referred Specimens– UALVP 31545a-b (Fig. 4-2A), SL=72, an incomplete part and counterpart from the "fish layer"; and UALVP 37128a-b (Fig. 4-2B), SL=50, an incomplete part and counterpart from layer 3 (Wilson and Williams, 1991).

Isolated bones: UALVP 15995, a nearly complete impression of the frontal from Joffre Bridge (Fig. 4-4A); UALVP 17242, a nearly complete preopercle from Joffre Bridge; UALVP 17846, 17852, two opercles from Joffre Bridge; UALVP 17847, 17848 (Fig. 4-4B), two nearly complete impressions of opercles from Robb Coal Mine, Alberta; UALVP 17068, 17317, 17327b, and 37136, four maxillae from Joffre Bridge; UALVP 15069 (Fig. 4-4C), 17024, 17853, 17854, four dentaries from Joffre Bridge; UALVP 17241, an incomplete parasphenoid; UALVP 17327a, a nearly complete tooth plate of the basihyal. All of these isolated elements were collected from layer 5 (Wilson and Williams, 1991).

Etymology– The specific name is based on the equal-sized dorsal and anal fins.

Type Locality– UALVP Locality No. 56: the "fish layer" at the Joffre Bridge road cut, 14 km east of Red Deer, Alberta, Canada (see Wilson and Williams, 1991: fig. 1).

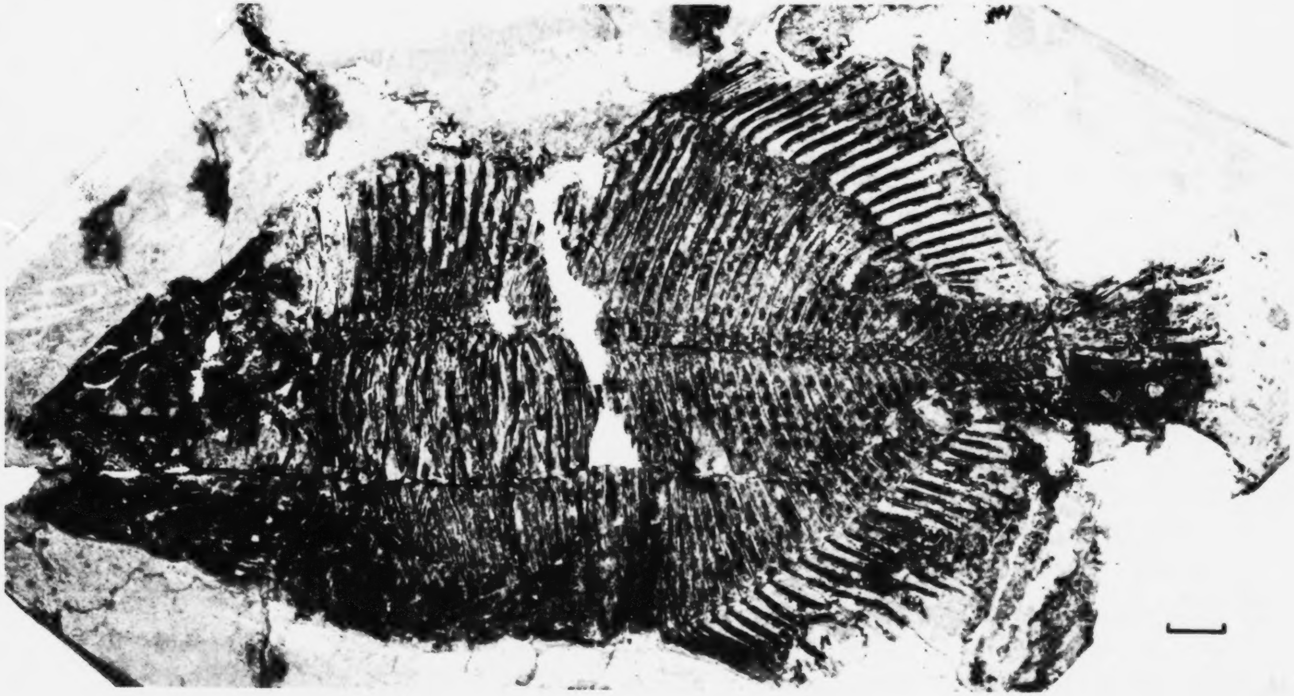


FIGURE 4-1: Photo of the holotype of †*Joffrichthys symmetroptera* gen. et sp. nov., taken from UALVP 23705a. Scale bar equals 5mm.

Horizon– The Lacombe Member of the Paskapoo Formation, Tertiary, Paleocene, middle Tiffanian (Ti3).

Description

The three articulated specimens suggest that this fish is moderately deep-bodied and laterally flattened with a relatively small head. The suboval body is proportionally and sharply decreased in its depth from the begins of the dorsal and anal fins to the ends of these two fins, with a short caudal peduncle (Fig. 4-1).

Measurements– **1.** UALVP 23705: SL=90, BD=46, HL=26, HD=30, PPL=29, PVL=39, PDL=56, PAL=52, CPL=11, CPD=10, DFBL=29, AFBL=32.

2. UALVP 31545: SL=72, BD=36, HL=23, HD=20, PPL=24, PVL=34, PDL=41, PAL=43, CPL=10, CPD= ~8, DFBL=22, AFBL=25.

3. UALVP 37128: SL=50, BD=25, HL=15, HD=16, PPL=14, PVL=22, PDL=28, PAL=31, CPL=9, CPD=7, DFBL=15, AFBL=14.

Meristics– **1.** UALVP 23705: BR=8, TV=51 (PCV 22 + CV 29), SN=18, PFR~11, VFR=3+ (incomplete), DFR=24, DP=25, AFR=24, AP=25, CFR=i+8+7+i, H=5 or 6, UN=0, EP=1.

2. UALVP 31545: BR=8, TV=51 (PCV 22+ CV 29), SN=16, PFR=12, VFR=6, DFR=24, DP=24, AFR=24, AP=25, CFR=i+8+7+i, H=6, UN=0, EP=1.

3. UALVP 37128: BR ~8, TV=48 (PCV22+CV26), SN=15, PFR=12, VFR=6, DFR=24, DP=25, AFR=24, AP=25, CFR=i+8+?, H=6, UN=0, EP=1.

Neurocranium and Skull Roof– This region is poorly preserved on all specimens with the exception of the bones comprising the skull roof. The supraoccipital is triangular from lateral view (UALVP 23705a). It develops a prominent occipital expansion that extends postero-dorsally to form a deep occipital crest. The anterior end of this bone extends slightly anteriorly to between the two parietals (Figs. 4-1 and 4-3).

The parietal is shorter than it is broad with a slightly curved anterior edge and a posteriorly somewhat lower dorsal edge (UALVP 23705 and 31545). The two parietals are possibly partly separated by the supraoccipital.

The frontal is longer than broad and irregularly trapezoidal in shape with its anterior end narrower than its posterior end. Judging from the right frontal preserved on UALVP 23705 and the isolated frontal on UALVP 15995, the orbital edge of this bone is slightly curved, and the suture between the two frontals is straight (Figs. 4-3 and 4-4A).

The nasal is somewhat subrectangular in shape and possibly tubular, the anterior supraorbital canal passes through it and ends in the nares.

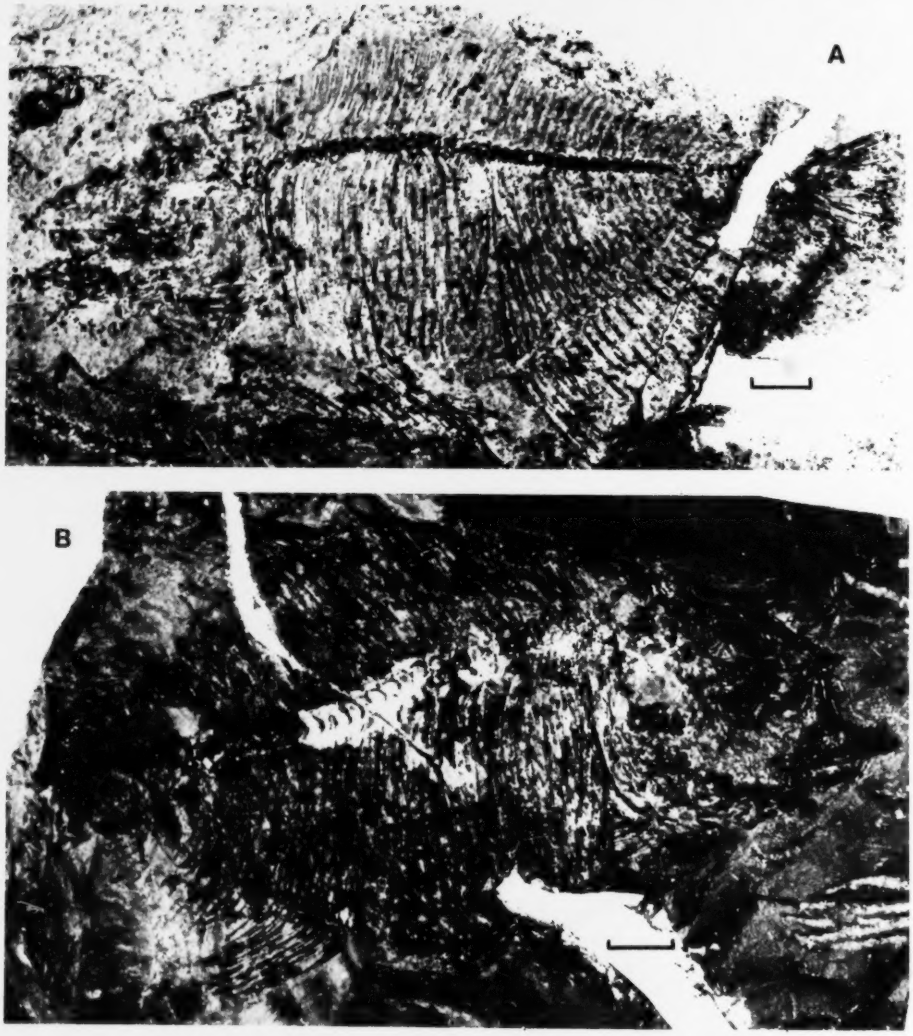


FIGURE 4-2. Two articulated specimens of †*Joffrichthys symmetroptera* gen. et sp. nov. **A,** UALVP 31545b; scale bar equals 5mm; **B,** UALVP 37128a; scale bar equals 4mm.

The mesethemoid is partly preserved on UALVP 23705. It seems not to separate the two nasals from the middle line of the skull roof.

The otic-temporal region can scarcely be described because of the poor preservation of this area. It is, however, rather certain that a temporal fenestra is absent in this fish.

The parasphenoid (UALVP 23705 and 31545) crossing the lower part of the orbit is knife-like in lateral view, with a strong dorsal crest. Its postero-medial portion is toothed, with strong conical teeth arranged in two rows. Both the ascending and occipital arms are developed on this bone. UALVP 17241, an incomplete parasphenoid, shows the same characters as that on 23705 and 31545. Although I am not sure whether the basipterygoid process is developed or not, this type of parasphenoid is rather different from that in *Heterotis*.

Orbital Region– The orbit is moderate in size, with a horizontal diameter approximately 6% of the standard length. The antorbital appears to be subsemicircular in shape, although it left only a vague impression on the specimen. The first and second infraorbitals are partly seen beneath the parasphenoid on UALVP 23705 and 31545; the former appears to be curved, elongated and anteriorly narrower than posteriorly, and the latter is somewhat widely trapezoidal in shape. Judging from the remnant of the infraorbital canal surrounding the orbit, there are also two large infraorbitals behind the orbit (Fig. 4-3), as in all other osteoglossomorphs. The dermosphenotic is poorly preserved on the holotype, but appears to be similar to that in *Heterotis*.

The supraorbital is absent, as in all other osteoglossomorphs.

Opercular System– The preopercle is poorly preserved on all three articulated specimens. Judging from the remnant on UALVP 23705a and the vague impression on UALVP 31545a, it is a wide "L"-shaped bone with a vertical arm nearly as long as but slightly narrower than the horizontal arm. The two arms form an angle of approximately 100° (Figs 4-3 and 4-4E). The preopercular canal passes through this bone along its frontal margin, giving off at least three branches at the horizontal arm. UALVP 17242, an isolated preopercle exposed from the inside, may be referred to this fish because it shows most of the features seen on the preopercle preserved on UALVP 23705 and 31545. This type of preopercle resembles that in the Recent *Heterotis*.

Characters of the opercle are recoverable by combining the features shown on the three articulated specimens. It is oval (UALVP 31545a) and radiately sculptured surficially (UALVP 23705a and 37128). Several isolated opercles referred to this fish [UALVP 17846, 17852 from Joffre Bridge, and UALVP 17847, 17848 (see Fig. 4-4B) from Robb Coal Mine, Alberta] confirm the characters shown on the poorly preserved opercle of 23705 and 31545. This type of opercle is similar to that in the Recent *Heterotis* and *Arapaima*.

The subopercle appears to be semilunar in shape, with a rounded ventral edge (UALVP 23705), and is similar to that in †*Phareodus* .

No information about the interopercle is obtainable from the specimens.

Jaws and Palatopterygo-quadrate Arch– As in the Recent *Heterotis* and *Arapaima*, the mouth cleft, constructed by the premaxilla, maxilla, and dentary, is shallower than that in other osteoglossomorphs. It does not extend posteriorly to beyond the anterior edge of the orbit.

The premaxilla appears to have the same pattern as that in †*Phareodus*. It is anteriorly deeper and posteriorly very shallow. Teeth on this bone are sharply conical, and arranged in two rows (Fig. 4-3).

The maxilla is completely preserved on UALVP 37128 (Fig. 4-4D). It is anteriorly gradually tapering with a pointed anterior end overlapping the posterior portion of the premaxilla. The posterior edge of the maxilla is smoothly rounded; it extends posteriorly to about the vertical midline of the orbit. Teeth are sharp, conical, and arranged in one row. These features are also seen on three isolated maxillae from Joffre Bridge (UALVP 17068, 17317, 17327b).

A supramaxilla is definitely absent.

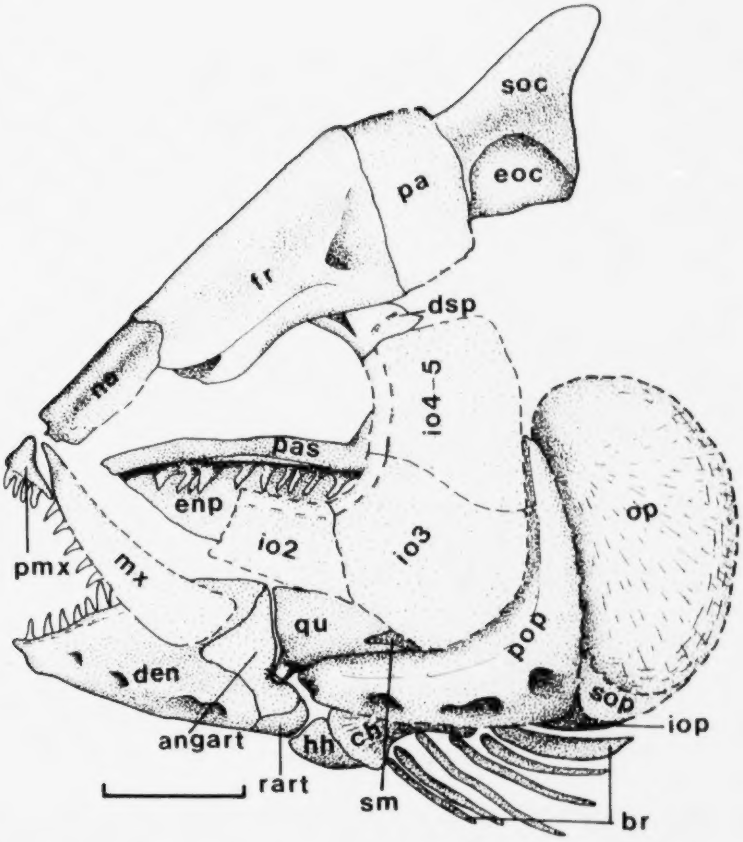
The dentary has a deep coronoid process posteriorly (UALVP 23705 and 37128; see Figs. 4-3 and 4-4D). A ridge that is parallel to the ventral edge of this bone is developed; through it passes the preoperculo-mandibular canal. Teeth are stronger than those on the premaxilla and maxilla and arranged in two rows. Four isolated dentaries from Joffre Bridge (UALVP 15069, 17024, 17853, and 17854) may be referred to this fish; of these, UALVP 15069 is almost complete, although it left only an impression (Fig. 4-4C; also see Wilson, 1980: fig. 1b)

The angular and articular seem to have been fused with each other, both contributing to the articulation facet for the quadrate.

The quadrate partly seen on three articulated specimens resembles that in *Heterotis* in shape and joins with the articular and angular of the lower jaw by a strong head.

The palatine and ectopterygoid have sharp conical teeth (UALVP 23705), but these bones are too poorly preserved to be described.

Hyoid Arch– It is difficult to give a detailed description of the hyomandibular because of the poor preservation of this bone. It resembles that in the extant *Heterotis* judgung by the remnant on UALVP 23705 and 31545.


soc
eoc
pa
fr
dsp
na
io4–5
pas
enp
io2
io3
op
pmx
mx
qu
pop
den
sop
iop
angart
hh
ch
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br

FIGURE 4-3: Partial restoration of the cranial skeleton of †*Joffrichthys symmetropterus* gen. et sp. nov., based on UALVP 23705. Scale bar equals 5mm.

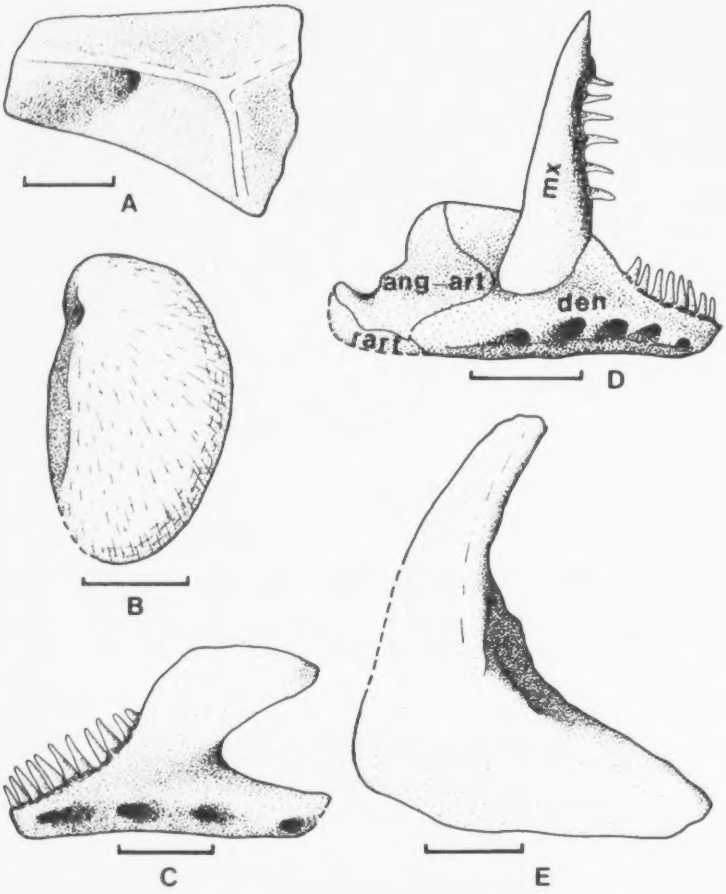


FIGURE 4-4: Disarticulated bones of †*Joffrichthys symmetropterus* gen. et sp. nov. **A**, frontal, UALVP 15995; **B**, opercle, UALVP 17848; **C**, dentary, UALVP 15069; **D**, lower and upper jaws, UALVP 37128, scale bar equals 2mm; and **E**, mesial view of preopercle, UALVP 17242. Scale bars for **A**, **B**, **C**, and **E** equal 5mm.

The ceratohyal is medially constricted and has the shape of the cross-section of a biconcave lens (UALVP 31545 and 37128). It is similar to that in *Heterotis* in having a ridged lateral surface (UALVP 23705 and 31545)

The hypohyal may consist of two parts, a dorsal hypohyal and a ventral hypohyal; both are irregular in shape (UALVP 31545 and 37128).

The basihyal appears to be triangular although it is poorly preserved on UALVP 31545. This bone inserts in the posterior notch of the tooth plate.

The tooth plate of the basihyal is well exposed on UALVP 37128. It is robust and triangular. Conical teeth on the margin are much larger than those in the central region (UALVP 31545 and 37128). An isolated tooth plate of the basihyal (UALVP 17327a) is considered to belong to this fish. This type of basihyal tooth plate closely resembles that in *Arapaima*.

Eight branchiostegals are developed (UALVP 23705 and 31545), of which the anterior four are slender and contact the ceratohyal.

Cephalic Lateral Line System– Judging from the poorly preserved specimens, the cephalic lateral line system is similar to that in Hiodontidae in its pattern. The supraorbital canal ends definitely in the parietal and may connect with the infraorbital canal through the canal in demosphenoid (UALVP 23705).

Vertebral Column– The vertebral column is completely ossified. It consists of 22 precaudal centra, which are higher than long, and 26 to 29 caudal vertebrae. Each of the centra is constricted at its middle and has one strong lateral ridge that makes the centrum looks like the latter "H" (UALVP 23705; Fig. 4-1).

Neural arches and neural spines are developed on both the precaudal and the caudal vertebrae; those on the caudals are fused with each other.

About 18 pairs of slender pleural ribs are present, extending from each of the precaudal centra to near the ventral wall of the body cavity. The slender haemal spines of the anterior preurals are partly overlapped by the anal pterygiophores.

Epineurals are present. These are fine paired elements that extend postero-dorsally from behind the base of the neural arches of the precaudal vertebrae.

Some 18 distally expanded supraneurals are counted on UALVP 23705; their proximal ends overlap the neural spines on the precaudal centra.

Caudal Skeleton– Caudal vertebrae involved in supporting the caudal fin consist of two upturned urals and three preurals.

Six hypurals are present (UALVP 23705b, impression; UALVP 37128b; Fig. 4-5), of which the two lower ones articulate with the first ural and support the lower lobe of the caudal fin, with the parhypural on the first preural and the haemal spines on the second to the third preurals. The four upper ones connecting with the second ural support the upper lobe of the caudal fin, with neural spines on the first ural and the first preural.

The neural spine on the first ural is strong and completely developed, as is that on the first preural. As in †*Phareodus* and some *Hiodon*, the second preural bears double fully developed neural spines that are slightly less strong than those on other preurals. All the neural spines on the caudal vertebrae are fused with the centra.

There is only one slender epural, which is involved in supporting the upper lobe of the caudal fin (Fig. 4-5).

The uroneurals are absent on all specimens, as in †*Phareodus* and all the extant osteoglossids.

Pectoral Girdle and Fin– The pectoral girdle is poorly preserved on all specimens. Only the shape of cleithrum may be reconstructed. It is sickle-shaped. Its lower limb extends antero-ventrally to form an angle of about 135° with its vertical upper limb.

The pectoral fin is larger than the pelvic fin. It consists of 12 fin rays (UALVP 31545 and 37128). As in the Recent *Heterotis* and *Arapaima*, the first pectoral ray is not greatly lengthened or thickened.

Pelvic Girdle and Fin– The innominatum forming the pelvic girdle is destroyed on all specimens. The pelvic fin is incompletely preserved on UALVP 23705. It is, however, visible on UALVP 31545 and 37128, where it is approximately half as large as the pectoral fin, and consists of six rays. The distance between the beginning of the pelvic fin and the beginning of the pectoral fin is slightly greater than that between the beginning of the pelvic fin and the beginning of the anal fin.

Dorsal and Anal Fins– The dorsal fin is roughly as large as the anal fin (Fig. 4-1), with a rounded distal edge and a base length approximately equal to 32% of the standard length, slightly shorter than that of the anal fin (UALVP 23705 and 31545; on UALVP 37128 the dorsal fin base length is slightly longer than the anal fin). It originates about four precaudal vertebrae anterior to the anal fin. In total, the fin contains 24 principal rays, of which the first is distally segmented but unbranched, and the last is double. These dorsal fin rays are supported by 24 (UALVP 31545) or 25 (UALVP 23705 and 37128) dorsal pterygiophores, of which the anteriormost inserts four vertebrae anterior to the anteriormost anal pterygiophore (UALVP 23705 and 31545).

The anal fin is large, with a base length approximately equal to 35% of the standard length, and resembles the dorsal fin in its shape (UALVP 23705 and 31545). It consists of 24 principal rays supported by 25 distally expanded anal pterygiophores. As in the

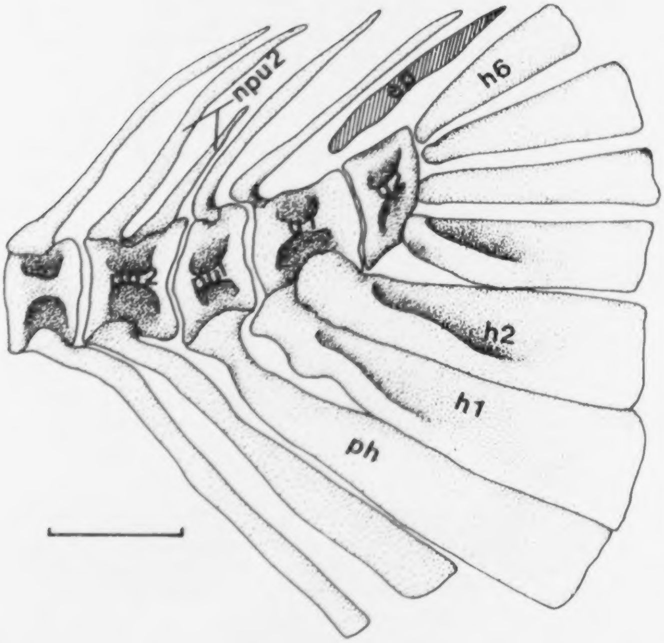

npu2
h6
pu2
pu1
h2
h1
ph

FIGURE 4-5: Restoration of the caudal skeleton of †*Joffrichthys symmetropterus* gen. et sp. nov., mainly based on UALVP 23705. Scale bar equals 2mm.

dorsal fin, both principal anal fin rays and anal pterygiophores are successively reduced in length from the first to the last (Fig. 4-1).

Caudal Fin– The caudal fin is distally incomplete on all the specimens. It is probably forked judging from the medial rays that are less thicker than the upper and lower principal rays. Counting impressions on UALVP 23705 and 31545, 17 principal caudal fin rays are seen; nine are involved in the formation of the lower lobe, and eight in the upper lobe. On UALVP 37128, the lower lobe also consists of nine principal rays.

Scales– Scales are well preserved in the caudal region of UALVP 23705. They are cycloid with the nucleus (focus) near to the centre. The fine growth lines are interrupted by seven to nine anterior (basal) radii. No reticulation is seen on any of the scales.

†*Joffrichthys* sp.

(Fig. 4-6 and 4-7)

Materials– UALVP 34770, an incomplete specimen with disarticulated jaws, opercle, subopercle, and some branchiostegals exposed as side-A (lateral view) and side-B (mesial view). UALVP 17843, 17844, 17845, 19517, four isolated opercles. UALVP 17059, 17319, two isolated dentaries. UALVP 17128, an incomplete parasphenoid.

Locality– Smoky Tower (UALVP 34770) and Joffre Bridge (all isolated bones).

Horizon– Joffre Bridge: Paskapoo Formation, late Paleocene, middle Tiffanian (Ti3). Smoky Tower: Paskapoo Formation, early to middle Paleocene.

Description

Preserved with the incomplete UALVP 34770 from the Paskapoo Formation of Smoky Tower locality are two small percopsid fishes on side-A and two esocoid fishes on side-B. Although this incomplete osteoglossid fish is more than two times as large as the holotype of †*Joffrichthys symmetropterus* gen. et sp. nov., the separate maxilla, dentary, opercle, and subopercle seen on side-A are indistinguishable from those of †*Joffrichthys symmetropterus* gen. et sp. nov.

The lower jaw is completely exposed on side-A of UALVP 34770. Posterior to the dentary are exposed the coronomeckelian and the articular that seems to have fused with the angular. A spacious articulation facet for the quadrate is constructed by the angulo-articular and the retroarticular that has a distinct posterior process (Fig. 4-7C).

The isolated opercle (UALVP 17843-17845, 19517), dentary (UALVP 17059 and 17319), and parasphenoid (UALVP 17128) from Joffre Bridge locality are comparable

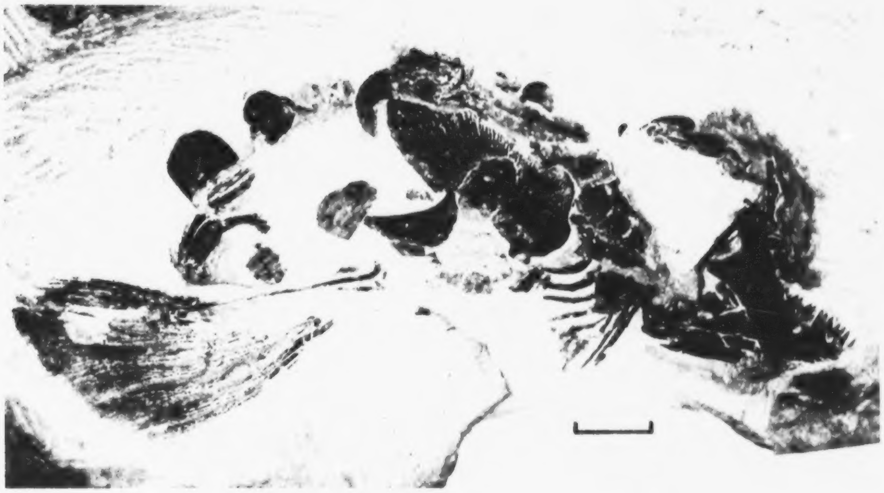


FIGURE 4-6: †*Joffrichthys* sp., photo of UALVP 34770, showing some of the disarticulated cranial elements. Scale bar equals 10mm.

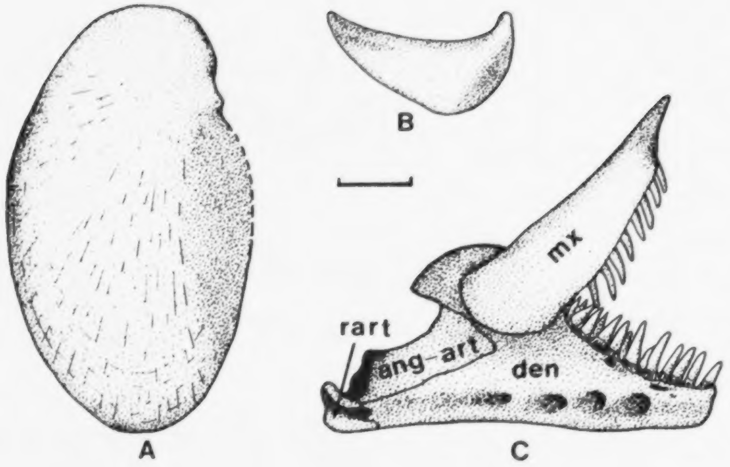

B
mx
rart
ang-art
den
A
C

FIGURE 4-7. †*Joffrichthys* sp., restoration of the disarticulated cranial elements on UALVP 34770. **A**, opercle; **B**, subopercle; and **C**, the lower and upper jaws. Scale bar equals 5mm.

with the corresponding element in †*Joffrichthys symmetropterus* gen. et sp. nov.

Nine branchiostegals are present on UALVP 34770 from Smoky Tower locality. The fourth is paired. This means that the whole set of the branchiostegals consists of also eight elements on each side as in †*Joffrichthys symmetropterus* gen. et sp. nov.

An incomplete pectoral fin is seen on side-A of UALVP 34770. It consists of 10 distally segmented and branched rays.

The proximal part of the pelvic fin is exposed on side-B, and consists of six rays.

A nearly complete dorsal fin is seen on side-B of UALVP 34770. This dorsal fin consists of at least 23 principal rays, of which the last one is double.

The broken anal fin is incompletely seen on side-B. It has at least 22 principal rays, of which the first one is distally segmented but not branched, and the others are both distally segmented and branched.

The caudal fin is distally incomplete, 18 principal rays were counted on side-B of UALVP 34770, suggesting that both lower and upper lobes consist of nine principal rays.

The characteristics shown by the scales on side-B of UALVP 34770 indicate that the scales are structurally the same as those in †*Joffrichthys symmetropterus* gen. et sp. nov.

Remarks– It seems quite certain that the materials described above can be referred to †*Joffrichthys* gen. nov. because all the observable character states except for the number of principal caudal fin rays are the same. The pattern of the opercle, the type of the lower and upper jaws even suggest that these disarticulated elements may belong to the same species of †*Joffrichthys symmetropterus* gen. et sp. nov. This suggestion, of course, needs to be confirmed in the future by finding better preserved materials. Further investigation should be made particularly at the Smoky Tower locality.

DISCUSSION

i. Taxonomic Setting of †*Joffrichthys* gen. nov.

It is evident that †*Joffrichthys* gen. nov. is an osteoglossomorph fish since it shares most of the synapomorphies defining the superorder Osteoglossomorpha, including a bite between the parasphenoid and basihyal, absence of supraorbital and supramaxilla, single epural, and 16 or 15 branched caudal fin rays.

Fig. 4-8 is the single shortest tree resulting from a cladistic analysis of 32 characters (Appendix 4-I) and their states in 12 representatives of Osteoglossomorpha (Table 4-1).

This tree shows clearly that †*Joffrichthys* is a new genus of Osteoglossiformes because it shares at least five of the six character states defining the clade: 2[1] (hypurals reduced to six), 3[1/2] (opercle oval or subsemicircular), 4[1] (absence of uroneural), 5[1] (at least one completely developed neural spine on u1), and 6[1] (17 principal caudal fin rays).

Further investigation suggests that this new osteoglossiform is a member of the Heterotidinae, closely related to the clade consisting of the Eocene-Oligocene †*Sinoglossus,* and the extant *Heterotis* and *Arapaima.* This sister-group relationship is strongly supported by at least five preserved skeletal features.

1. Posterior end of maxilla lying on dentary part of lower jaw (= 23[1]): My study indicates that this is one of the most important synapomophies shared by the species included in the subfamily Heterotidinae. Almost all the other osteoglossomorphs have a maxilla that lies posteriorly on the angular part of the lower jaw (see Ridewood, 1904, 1905; Roellig, 1967, 1974; Kershaw, 1976; Taverne, 1972, 1977, 1978). A maxilla with its posterior end lying on the angular part of the lower jaw is commonly seen in basal teleosts (see Arratia, 1987, 1994; Arratia and Schultze, 1991; Nybelin, 1974), in elopomorphs (see Forey, 1973), and in clupeomorphs (see Grande, 1985) as well as in euteleosts (see Gregory, 1933; Wilson and Williams, 1991).

The posterior end of the maxilla in †*Joffrichthys* gen. nov. lies on the dentary part of the lower jaw. This character state is here considered to be the most imporant evidence linking this new genus to the Heterotidinae.

2. Horizontal arm of preopercle about as long as vertical arm (= 24[1]): All the known species in Heterotidinae have a preopercle that has a horizontal arm as long as or even longer than the vertical arm (Figs. 4-9 and 4-10) (also see Ridewood, 1905; Kershaw, 1976; Su, 1986). The preopercle in †*Joffrichthys* gen. nov. is in the same pattern as that in *Heterotis*, *Arapaima*, and †*Sinoglossus*, which has a horizontal arm nearly as long as the vertical arm (e.g. UALVP 17242) (Figs. 4-3 and 4-4E); while the horizontal arm of the preopercle in all other known osteoglossomorph fishes is much shorter than the vertical arm (see Ridewood, 1904; Cavender, 1966; Taverne, 1972, 1977, 1978; Wilson, 1977, 1978a; Grande, 1979, 1984; Li, 1987).

3. Io2 relatively large and in the shape of an irregularly wide trapezoid (= 25[1]): Among previously named osteoglossiforms, a relatively large, wide, and trapezoidal io2 is only seen in *Heterotis*, *Arapaima*, and †*Sinoglossus* (Fig. 4-3). †*Joffrichthys* gen. nov. is the fourth genus having this type of io2. The io2 in all the other osteoglossomorphs is either small (e.g., that in *Hiodon*) or subrectangular (e.g.,

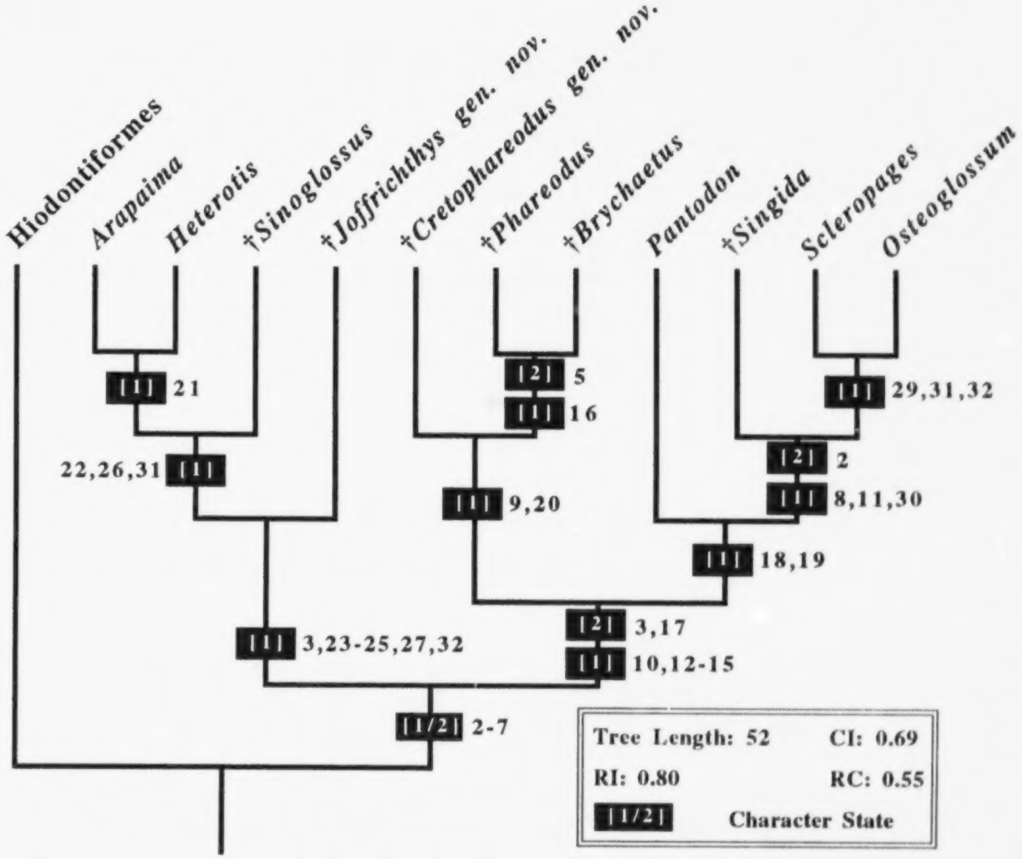

Hiodontiformes
Arapaima
Heterotis
†Sinoglossus
†Joffrichthys gen. nov.
†Cretophareodus gen. nov.
†Phareodus
†Brychaetus
Pantodon
†Singida
Scleropages
Osteoglossum
[1] 21
22,26,31 [1]
[2] 5
[1] 16
[1] 9,20
[1] 29,31,32
[2] 2
[1] 8,11,30
[1] 18,19
[2] 3,17
[1] 10,12-15
[1] 3,23-25,27,32
[1/2] 2-7
Tree Length: 52
CI: 0.69
RI: 0.80
RC: 0.55
[1/2] Character State

FIGURE 4-8: The single shortest tree generated by PAUP 3.1.1, showing the possible phylogenetic relationships among †*Joffrichthys* gen nov. and other osteoglossids. Characters represented by numbers are listed in Appendix 4-I. Their states (in square brackets in this diagram) are shown in Table 4-1.

TABLE 4-1: Data matrix showing the distribution of 32 characters and their states in the Osteoglossidae. Characters represent by numbers are listed in Appendix 4-1.

TAXA CHARACTERS AND THEIR STATES		Hiodontiformes	*Arapaima*	*Heterotis*	†*Sinoglossus*	†*Joffrichthys* gen. nov.	†*Brychaetus*	†*Phareodus*	†*Cretophareodus* gen. nov.	*Pantodon*	†*Singida*	*Scleropages*	*Osteoglossum*
1	TP	0	0	1	?	0	1	0	?	0	1	0	0
2	#H	0	1	1	?	1	?	1	?	1	2	2	2
3	Op	0	1	1	1	1	2	2	2	2	2	2	2
4	Un	0	1	1	?	1	?	1	?	1	0	1	1
5	Nu1	0	1	1	?	1	?	2	?	1	1	1	1
6	Pcfr	0	1	1	1	1	?	1	?	1	1	1	1
7	Io4-5	0	1	1	1	1	1	1	?	1	1	1	1
8	Nana	0	1	1	1	1	0	0	?	0	1	1	1
9	Bs	0	0	0	0	1	1	1	1	0	0	0	0
10	Bhbb	0	0	0	?	0	?	1	?	1	?	1	1
11	Pmop	0	0	0	0	0	0	0	0	0	1	1	1
12	Nape	0	0	0	0	?	1	1	?	1	?	1	1
13	Hap	0	0	0	0	0	1	1	1	1	1	1	1
14	Pomc	0	0	0	0	0	1	1	1	1	1	1	1
15	Pfr1	0	0	0	0	0	1	1	1	1	1	1	1
16	Hm	0	0	0	0	0	1	1	0	0	0	0	0
17	JA	1	0	0	0	0	2	2	2	2	2	2	2
18	Dmc	0	0	0	0	0	0	0	0	1	1	1	1
19	Popc	0	0	0	0	0	0	0	0	1	1	1	1
20	Fr	0	0	0	0	0	1	1	1	0	0	0	0
21	Tpb	0	1	1	0	0	?	0	?	0	?	0	0
22	Aio1	0	1	1	1	?	0	0	0	0	0	0	0
23	Pemx	0	1	1	1	1	0	0	0	0	0	0	0
24	Lvap	0	1	1	1	1	0	0	0	0	0	0	0
25	Io2	0	1	1	1	1	0	0	0	0	0	0	0
26	CKW	0	1	1	1	?	0	0	0	0	0	0	0
27	AF	0	1	0	1	1	0	0	1	0	0	0	0
28	Uhu2	0	1	1	?	0	?	0	?	1	0	1	1
29	SDF	0	1	1	1	1	?	1	1	0	0	1	1
30	Npu1	0	0	0	?	1	?	0	?	0	1	1	1
31	Sc	0	1	1	1	0	0	1	0	0	0	1	1
32	Prda	0	1	1	1	1	?	1	1	0	0	1	1

that in *Osteoglossum*) (pers. obs.; also see Nelson, 1969) or slender (e.g., that in Mormyroidea) (Taverne, 1972).

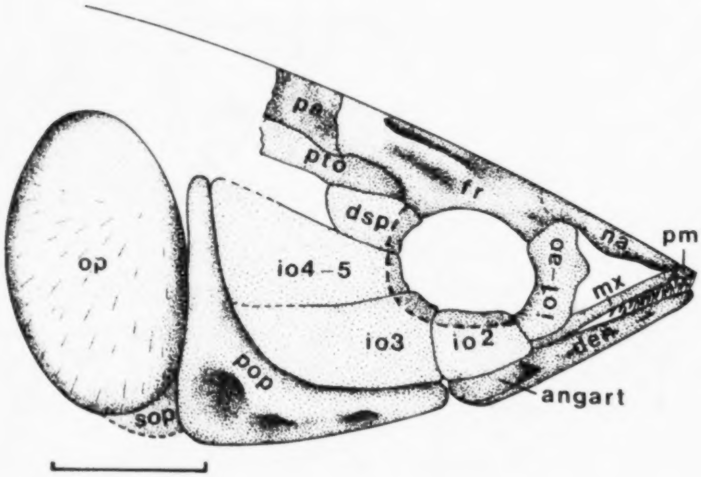
4. Anal fin as large as or more or less smaller than dorsal fin (= 27[1]): The anal fin in basal teleosts (see Arratia, 1987, 1994; Nybelin, 1974), elopomorphs (see Forey, 1973), clupeomorphs (see Grande, 1985), and most euteleosts (see Nelson, 1994; Wilson and Williams, 1991) is usually larger than the dorsal fin. A similar condition is seen in most of the other osteoglossomorphs with a posteriorly located dorsal fin. In contrast, all species referred to Heterotidinae have an anal fin that is nearly as large as the dorsal fin (e.g. *Arapaima*) or distinctly smaller than the dorsal fin (e.g. †*Sinoglossus*). The anal and dorsal fins in †*Joffrichthys* gen. nov. are not only equal in size but also are supported by the same number of pterygiophores. This character state may be another important synapomorphy of Heterotidinae.

5. Posterior dorsal and anal fin rays longer than or about as long as anterior rays (= 32[1]): Another possible synapomorphy linking †*Joffrichthys* gen. nov. to the clade Heterotidinae is from the posterior rays of the dorsal and anal fins, which are longer than or about as long as the anterior rays of the two median fins (= 32[1]). Although this character state is highly homoplastic in Osteoglossompha because of its presence in the Eocene †*Phareodus* and the extant *Osteoglossum* and *Scleropages*, it is still considered to be an important synapomorphy of Heterotidinae since it is shared by all the known species including †*Joffrichthys* gen. nov. placed in Heterotidinae.

It is noticeable that two other important character states need to be confirmed in †*Joffrichthys* gen. nov. in the future. One concerns the relationship between the antorbital and the first infraorbital. In the available material, I am not sure whether the antorbital has fused with the first infraorbital in †*Joffrichthys* gen. nov. as it has in *Heterotis*, *Arapaima*, and †*Sinoglossus*. The other concerns the "cheek wall" formed by the enlargement of the first to the third infraorbitals. Judging from the relatively large io2, a "cheek wall" appears to be present in †*Joffrichthys* gen. nov.

ii. Comments on Early Evolution of Heterotidinae

Unlike the subfamily Osteoglossinae, there was no fossil representative directly referred to the Heterotidinae in the world before the discovery of †*Joffrichthys* from the Paleocene Paskapoo Formation of Alberta. A comparison among †*Joffrichthys* and the previously named fossil and extant osteoglossid genera suggests a possible evolutionary lineage consisting of †*Joffrichthys* gen. nov., †*Sinoglossus*, *Heterotis*, and *Arapaima*. Among these genera, †*Sinoglossus* was originally supposed to be more closely related to


pa
pto
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io4-5
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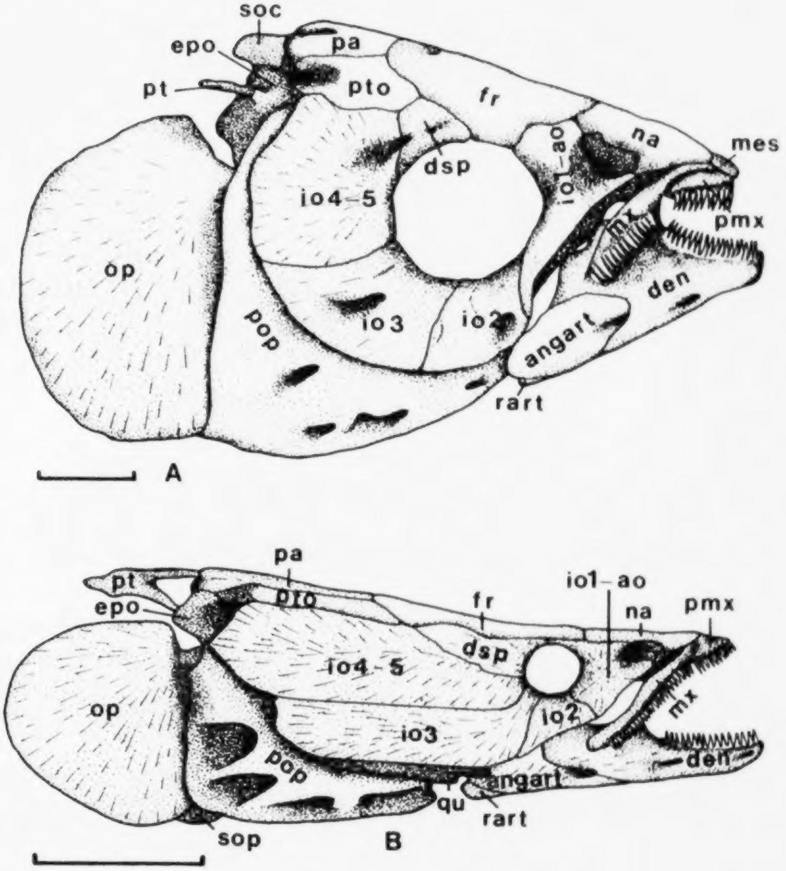
FIGURE 4-9: Partial restoration of the cranial skeleton of †*Sinoglossus lushanensis*, modified from Su (1986). Scale bar equals 10mm.


soc
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B

FIGURE 4-10: Cranial Skeleton of *Heterotis niloticus* (**A**) and *Arapaima gigas* (**B**), modified from Ridewood (1905). Scale bar for **A** equals 10mm; and for **B** 80mm.

Osteoglossum and *Scleropages* than to other Recent osteoglossids (Su, 1986). My study indicates that the presumed †*Sinoglossus-Scleropages-Osteoglossum* relationship is not valid. As shown in Fig. 4-8, †*Sinoglossus* is most closely related to the Recent *Heterotis* and *Arapaima*. It takes the position of the sister-group of the clade consisting of *Heterotis* and *Arapaima*. At least six synapomorphies have been found to be particularly significant in supporting the heterotidine relationship of †*Sinoglossus*: 1) 23[1], the posterior end of the maxilla lies on the dentary part of the lower jaw. 2) 24[1], the horizontal arm of the preopercle is as long as the vertical arm. 3) 25[1], the second infraorbital is large and widely trapezoidal in shape. 4) 26[1], io1 to io3 are enlarged to form a "cheek wall." Unlike the "infraorbital ledge" in Notopteridae, the "cheek wall" in Heterotidinae covers all the area below the orbit from the antorbital to the anterior edge of the preopercle. 5) 27[1], the anal fin is smaller than the dorsal fin. 6) 32[1], the posterior rays of the dorsal and anal fins are longer than the anterior rays. These six synapomorphies closely link †*Sinoglossus* with *Heterotis* and *Arapaima*, as well as †*Joffrichthys* gen. nov. in a monophyletic group.

As regards the sister-group relationship between †*Sinoglossus* and the extant *Heterotis* plus *Arapaima*, it is, at present, supported by at least two synapomorphies: fusion of the antorbital with the first infraorbital (= 22[1]) and a "cheek wall" formed by io1 to io3 (=26[1]). So far as I know, in all of the previously named osteoglossomorphs, an antorbital fused with the first infraorbital and a typical "cheek wall" are seen only in †*Sinoglossus*, *Heterotis*, and *Arapaima*. They are here considered to be the most important synapomorphies linking these three genera in a clade.

As for the early evolution of Heterotidinae, evidence remains inconclusive. However, two Late Jurassic-Early Cretaceous eastern Asian teleosts [†*Huashia* Chang and Chou, 1977 (also see Ma, 1986) and †*Kuntulunia* Liu et al., 1982 (also see Zhang, 1990) and one mid-Cretaceous South American primitive osteoglossomorph (†*Laeliichthys* Santos, 1985) might have some relationship with the ancestral lineages or sister-group of Heterotidinae. This possibility is suggested by the following conbination of character states: (1) plate-like nasal, (2) shortened frontal broadest above the orbit, (3) anteriorly somewhat rectangular premaxilla, (4) bent maxilla with a posterior end extending back to only slightly beyond the anterior edge of the orbit and lying mainly on the dentary part of the lower jaw, (5) dentary posteriorly much deeper than anteriorly to form a deep coronoid process, (6) mouth corner located anterior to the orbit, (7) horizontal arm of preopercle nearly as long as the vertical arm, (8) opercle oval, (9) similar type of hyomandibular with a nearly square antero-ventral wing, (10) preoperculo-mandibular canal giving off three branches on the horizontal arm of the preopercle. Futher investigation of these character states may help clarify the possible relationships among Heterotidinae and the three above-mentioned Late Mesozoic primitive teleosts.

CONCLUSION

The new Paleocene osteoglossid genus †*Joffrichthys* is characterized by a pair of small pectoral fins, the symmetrical dorsal and anal fins consisting of the same number of principal rays and supported by the same number of pterygiophores, "H"-shaped caudal vertebrae, and cycloid scales with nearly central foci but no reticulation.

A close relationship between †*Joffrichths* gen. nov. and Heterotidinae is strongly suggested by (1) the posterior end of the maxilla lying on the dentary part of the lower jaw, (2) a preopercle that has a horizontal arm nearly as long as the vertical arm, (3) the second infraorbital relatively large and irregularly wide trapezoidal, (4) anal fin as large as the dorsal fin, and (5) the posterior rays of the dorsal and anal fins longer than or about as long as the anterior rays of the two median fins.

The eastern Asian Eocene-Oligocene †*Sinoglossus* is one of the members of Heterotidinae because it shares all the synapomorphies of Heterotidinae. Two features (io1 fused with antorbital and a "cheek wall" formed by io1 to io3 and covering all the area below the orbit from the antorbital to the anterior edge of the preopercle) even suggest that †*Sinoglossus* is the sister-group of the clade consisting of *Heterotis* and *Arapaima*.

Further investigation of two Late Jurassic-Early Cretaceous eastern Asian primitive teleosts (†*Huashia* and †*Kuntulunia*) and one mid-Cretaceous South American osteoglossomorph (†*Laeliichthys*) may be able to clarify the early evolution of the Heterotidinae.

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APPENDIX 4-I

32 characters used in cladistic analysis are

1. Teeth on parasphenoid: (TP)
   [0] = present
   [1] = absent

2. Number of hypural: (#H)
   [0] = seven or more
   [1] = six
   [2] = five or fewer

3. Opercle: (Op)
   [0] = irregular parallelogram
   [1] = oval or somewhat kidney-shaped
   [2] = subsemicircular

4. Uroneurals: (Un)
   [0] = present
   [1] = absent

5. Neural spine on u1: (Nu1)
   [0] = absent or rudimentary
   [1] = one complete
   [2] = double

6. Principal caudal fin rays: (Pcfr)
   [0] = eighteen or more
   [1] = seventeen or fewer

7. 4th and 5th infraorbitals: (Io4-5)
   [0] = separate from each other
   [1] = fused

8. Relationship between two nasals: (Nana)
   [0] = separated by mesethmoid
   [1] = meeting with each other

9. Body shape: (Bs)
   [0] = fusiform
   [1] = oval or deep with a large abdominal cavity

10. Basihyal tooth plate and basibranchial tooth plate: (Bhbb)
    [0] = separate from each other
    [1] = fused with each other

11. Postero-ventral margin of opercle: (Pmop)
    [0] = rounded
    [1] = distinctly concave

12. Posterior edge of the nasal: (Nape)
    [0] = straight or slightly curved
    [1] = strongly curved and extending backward

13. Horizontal arm of preopercle: (Hap)
    [0] = extending anteriorly to beneath orbit
    [1] = extending anteriorly behind the orbit

14. Branches of preoperculo-mandibular canal on horizontal arm of preopercle: (Pomc)
    [0] = distributed as separate openings
    [1] = connected with each other to form a horizontal groove

15. First pectoral fin ray: (Pfr1)
    [0] = normal
    [1] = strong and extremely long

16. Hyomandibular: (Hm)
    [0] = anterior not much expanded
    [1] = with a greatly expanded subtriangular anterior wing

17. Jaw articulation (angle of jaws): (JA)
    [0] = anterior to the orbit
    [1] = beneath the orbit (1)
    [2] = behind the orbit

18. Direction of mouth cleft: (Dmc)
    [0] = anteriorly directed
    [1] = strongly upturned

19. Postero-ventral corner of preopercle: (Popc)
    [0] = rounded
    [1] = angulate

20. Frontal: (Fr)
    [0] = anteriorly narrower or only slightly broader than posteriorly
    [1] = anterior portion about twice as broad as posterior portion

21. Tooth plate on basihyal: (Tpb)
    [0] = present
    [1] = absent

22. Antorbital and the first infraorbital: (Aio1)
    [0] = separate from each other
    [1] = fused with each other

23. Posterior end of maxilla: (Pemx)
    [0] = lying on angular
    [1] = lying on dentary part

24. Length of vertical arm of preopercle: (Lvap)
    [0] = much longer than horizontal arm

[1] = about as long as horizontal arm

25. The second infraorbital: (Io2)
[0] = small and slender
[1] = large and irregularly wide trapezoidal in shape

26. "Cheek wall" formed by enlargement of 1st to 3rd infraorbitals: (CKW)
[0] = absent
[1] = present

27. Anal fin: (AF)
[0] = larger than dorsal fin
[1] = smaller than or as large as dorsal fin

28. Upper hypurals and the second ural: (Uhu2)
[0] = not fused
[1] = fused

29. Shape of dorsal fin: (SDF)
[0] = triangular
[1] = rounded

30. Number of neural spines on pu1 (if present): (Npu1)
[0] = one
[1] = double

31. Scales: (Sc)
[0] = not reticulate
[1] = reticulate

32. Posterior rays of dorsal and anal fins: (Prda)
[0] = shorter than anterior ones
[1] = longer than or nearly as long as anterior ones

Chapter 5

NEW MATERIALS OF †*EOHIODON* FROM WESTERN NORTH AMERICA, WITH A TAXONOMIC REASSESSMENT OF HIODONTIDAE AND NOTOPTERIDAE

INTRODUCTION

Since Cavender (1966) named †*Eohiodon* based on a review of Hussakof's (1916) "†*Leuciscus*" *rosei,* three North American species have been included in this Eocene genus (see Table 1-1). †*Eohiodon rosei* (Hussakof) Cavender (1966) is mainly known in the Tranquille Bed near Kamloops, in the Allenby Formation near Princeton, and in the Horsefly beds near Horsefly of British Columbia, Canada (Wilson, 1974, 1977, 1978). †*Eohiodon woodruffi* Wilson (1978) has been found in the Klondike Mountain Formation near Republic, Washington, USA, as well as in the Horsefly beds near Horsefly, British Columbia. †*Eohiodon falcatus* Grande (1979) is known from the Green River Formation of Lincoln County, Wyoming, USA.

Both †*Eohiodon woodruffi* and †*Eohiodon falcatus* were named on a few poorly preserved specimens, from which many important characters are missing. During the last decade, many new specimens of †*Eohiodon* (e.g., Figs. 5-1 and 5-2) have been collected from the Horsefly beds of British Columbia and the Fossil Butte Member of the Green River Formation of Wyoming. These new materials provide me with a chance to make a supplementary description of the previously named †*Eohiodon* species, and suggest that the two species of †*Eohiodon* are hardly distinguishible from each other on morphological grounds. †*Eohiodon falcatus* differs from †*Eohiodon woodruffi* only in having slightly more anal fin rays and anal pterygiophores. Therefore I am doubtful of the validity of †*Eohiodon falcatus.*

Another problem that has always plagued the study of the North American fossil hiodontids is the systematic position of *Hiodon*. The problem is whether or not Hiodontidae should be included in the suborder Notopteroidei with the extremely specialized family Notopteridae (Gosline, 1960; Greenwood, 1963, 1970; McAllister, 1968). This question has become even more difficult since Greenwood (1970) placed †Lycopteridae, an eastern Asian family of Late Jurassic to Early Cretaceous primitive teleosts, together with Hiodontidae in the suborder Notopteroidei (Grande, 1979; Taverne, 1979; Shen et al., 1991). These controversies may result from a mistaken linkage of *Notopterus* with *Hiodon*, suggested first by Bridge (1900), and then followed by Regan (1909) and Berg (1940), based on the so-called "swim bladder-ear connection," which is a highly homoplastic feature present in Hiodontidae, Notopteridae, Mormyroidea (Greenwood, 1973), and some clupeomorphs (Grande, 1985). Most recently, Gaudant (1988) suggested a possible relationship between †*Thaumaturus* and Hiodontidae. It therefore seems to me that clarification of the phylogeny of Hiodontidae and Notopteridae within the clade Osteoglossomorpha has become urgent.

This chapter will concentrate on (1) making a detailed supplementary description of †*Eohiodon woodruffi* and (2) reexamining the relationship between Hiodontidae and Notopteridae.

Comparative Materials

†Lycopteriformes– †Lycopteridae: †*Lycoptera davidi* (Sauvage), specimens including those listed in Liu et al. (1963), Ma (1987), and AMNH FF19400, 19403. †*Tongxinichthys microdus* Ma, specimens listed in Ma (1980).

Hiodontiformes *sensus stricto*– Hiodontidae: *Hiodon tergisus* and *Hiodon alosoides,* specimens listed in Chapter 6. †*Eohiodon rosei* (Hussakof), UALVP 12436 and specimens listed in Cavender (1966). †*Eohiodon woodruffi* Wilson, specimens listed in Wilson (1978). †*Eohiodon falcatus* Grande, specimens listed in Grande (1979). †*Yanbiania wangqingica* Li, specimens listed in Li (1987). †*Plesiolycoptera daqingensis* Zhang and Zhou, specimens listed in Zhang and Zhou (1976).

Osteoglossiformes– Osteoglossidae: *Osteoglossum bicirrosum* and *O. ferreirai*, specimens listed in Chapter 2. †*Phareodus testis* and †*Phareodus encaustus*, specimens studied in Chapter 2. †*Phareodus queenslandicus*, specimens listed in Chapter 2. *Arapaima gigas*, specimens listed in Chapter 2. †*Sinoglossus lushanensis* Su, specimens listed in Su (1986).

Pantodontidae: *Pantodon buchholsi*, specimens listed in Chapter 2

Notopteridae: *Notopterus chitali* and *Xenomystus nigri*, specimens used in Chapter 2.

SYSTEMATIC PALEONTOLOGY

Subdivision Teleostei Müller, 1846
Superorder Osteoglossomorpha Greenwood et al., 1966
Order Hiodontiformes *sensu stricto*

Included Family– Hiodontidae Valenciennes, 1846.

Emended Diagnosis– Osteoglossomorphs differing from †Lycopteriformes and Osteoglossiformes in having: dermosphenotic triradiate, dorsal part of hyomandibular separate or double-headed and bridged, opercle irregular parallelegram, dorsal arm of post-temporal more than twice as long as ventral arm, pelvic fin seven-rayed.

Family Hiodontidae Valenciennes, 1846

Type Genus– *Hiodon* Lesueur, 1818.

Included Genera– *Hiodon* Lesueur, 1818; †*Eohiodon* Cavender, 1966; †*Plesiolycoptera* Zhang and Zhou, 1976; †*Yanbiania* Li, 1987.

Diagnosis– Same as that for the order.

Remarks– Jin (1991) named an Early Cretaceous osteoglossomorph, †*Tanichthys*, based on material from eastern Shandong Province, China. He placed that genus in Hiodontidae on the basis of (1) absence of supraorbital, (2) absence of supramaxilla, (3) presence of two large posterior infraorbitals (= io3 and io4-5 in this thesis), (4) normal (not extremely strong and lengthened) first pectoral fin ray, and (5) number of (15-17) anal fin rays. Of these five character states used by Jin to establish the phylogeny of †*Tanichthys*, (1) to (3) are three of the eight important synapomorpbies defining the monophyly of Osteoglossomorpha (see Chapter 7); (4) is highly homoplastic, and is commonly seen in all the other osteoglossomorph fishes except Osteoglossinae; and (5) is at most an autapomorphy of †*Tanichthys*, and hence hardly significant in phylogenetic analysis. It is, thus, evident that all the character states used by Jin are invalid to support the hiodontid relationship of †*Tanichthys*. Since †*Tanichthys* does not share any of the five synapomorphies defining the monophyly of Hiodontiformes *sensus stricto* (coextensive with Hiodontidae), its placement in Hiodontidae is considered to be unsupported.

However, †*Tanichthys* is still an osteoglossomorph because it shares all the skeletal osteoglossomorph synapomorphies with other osteoglossomorphs (see Chapter 7).

Based on Jin's description and illustrations of †*Tanichthys*, it appears to be most closely related to †*Paralycoptera* Chang and Chou, 1977. These two East Asian Early Cretaceous primitive teleosts may together represent a stem-group of the Osteoglossiformes because they share at least three possible osteoglossiform synapomorphies (six hypurals, oval or subsemicircular opercle, and pterygo-quadrate area behind and below the orbit completely covered by infraorbitals).

Genus †*Eohiodon* Cavender, 1966

Type Species– †*Eohiodon rosei* (Hussakof, 1916), Cavender, 1966

Included Species– †*Eohiodon rosei* (Hussakof) Cavender, 1966; †*Eohiodon woodruffi* Wilson, 1978.

Emended Diagnosis– Hiodontidae differing from other genera in the family in the following character states: hyomandibular with three equal-sized dorsal parts (two cranial and one opercular process), TV 44-50 (PCV 22-24 + CV 23-26), DFR 11-15, DP 13-17, AFR 14-24, AP 16-25.

†*Eohiodon woodruffi* Wilson, 1978

(Figs. 5-1 to 5-5)

–†*Eohiodon falcatus* Grande, 1979

Emended Diagnosis– †*Eohiodon* differing from †*E. rosei* in having an anteriorly slender maxilla, and a dorsally and posteriorly slightly excavated opercle. TV 46-50 (PCV 23-24 + CV 23-26); DFR 12-14, DP 14-17; AFR 16-24, AP 17-25.

Holotype– UALVP 13227a-b, part and counterpart of a nearly complete fish, SL=108, collected by M. V. H. Wilson and L. A. Lindoe in 1976 from Tom Thumb Mine, near Republic, Washington, USA.

Referred New Specimen– This study is based on the new specimens from the following localities.

1) UALVP Locality No. 66, Horsefly Mine H1, British Columbia: UALVP 37135, an incomplete fish.

2) UALVP Locality No. 67, Horsefly Mine H2, British Columbia: UALVP 22905a-b, part and counterpart of a presumed female individual with an incomplete caudal fin, SL=128; UALVP 22917a-b, part and counterpart of the anterior portion of a fish;

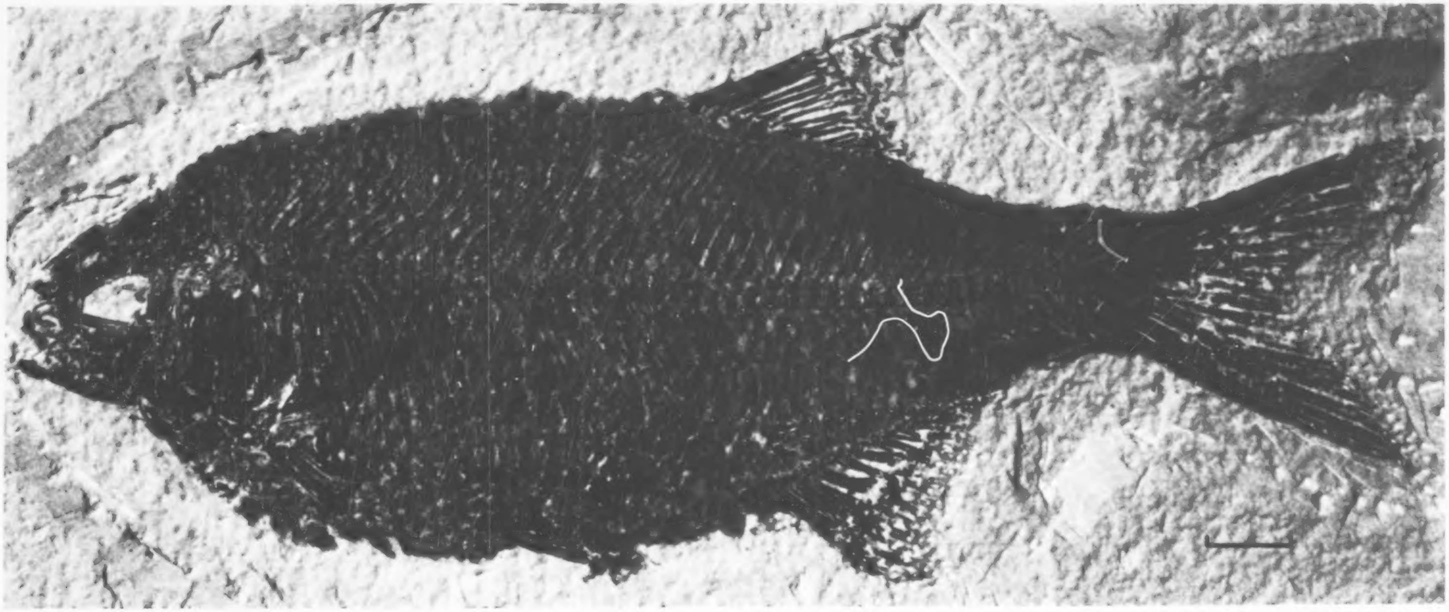

FIGURE 5-1: FMNH PF9882 (presumed female), one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming. Scale bar equals 10mm.

UALVP 31948a-b, part and counterpart of a nearly complete male, SL=185; and UALVP 31960 (SL=120) and 31966 (SL=115), two incomplete fishes. These five specimens were collected during the 1986 to 1988 field seasons.

3) UALVP Locality No. 68, Horsefly Mine H3, British Columbia: UALVP 31166, an incomplete fish. UALVP 15889a-b, opercular series; UALVP 15890, 17490, 17492, and ROM 11062, four incomplete fish.

4) UALVP Locality No. 55, Tunnel Creek, Montana: UALVP 24135 (SL=78) and UALVP 37129 (SL=71), two nearly complete skeletons.

5) UALVP Locality No. 87, Tynsky Quarry, Kemmerer, Lincoln County, Wyoming: Eight nearly complete or relatively well-preserved skeletons: FMNH PF9878, 9880, 9882 (Fig. 5-1), 10424, 10634, 10639, 12516 (Fig. 5-2 and 5-5), and ROM 43220; and eight incomplete specimens: FMNH PF9879, 10633, 10635, 10638, 10955, 13063, 13064, and UALVP 24203.

Horizon of Referred New Specimens– Specimens from (1) to (3) are found in Horsefly beds of Tertiary, middle Eocene age; specimens from (4) in Keshenehn Formation of Tertiary, late Eocene; and specimens from (5) in Fossil Butte Member of the Green River Formation, late early Eocene.

Remarks– FMNH PF10424 from UALVP Locality No. 87 was designated as the holotype of †*Eohiodon falcatus* by Grande in 1979, and was originally cataloged in the paleontological collections of the Department of Geology and Geophysics, University of Minnesota. It was later transferred to the paleontological collection of the Department of Geology, Field Museum of Natural History (Grande, 1991). The University of Minnesota number UAMVP 6499 has been changed to FMNH PF10424.

Description

Body Shape and Size– The body is fusiform and shallow in lateral view, with its maximum depth immediately in the front of the pelvic fins (Fig. 5-1). The juveniles appear to be more slender than the adults. As pointed out by Wilson (1978), all of the specimens discovered to date are laterally preserved, indicating a laterally compressed body in life. The adults may have a total length approaching or exceeding 200mm (UALVP 31948).

Measurements of Specimens– Appendix 5-I lists the data available to me at this time. The ranges of the various measurements are as follows. TL=38-217, FL=35-206, SL=30-182, BD=9-65, HL=8-43, HD=8-39, PPL=9-37, PVL=16-83, PDL=18-100, PAL=22-114, CPL=5-33, CPD=3-25.

Meristics of Specimens– Table 5-2 gives the following meristic ranges: PCV=23-24 (24 on Green River spceimens), CV=23-26 (25-26 on Green River specimens), TV=46-50 (49-50 on Green River specimens), BR=8-10 (mainly 8 on Green River specimens), PFR=12-13, VFR=7, DFR=12-14, DP=14-17, AFR=16-24 (21-24 on Green River specimens), AP=17-25 (21-25 on Green River specimens), CFR=i+8+8+i, SPN=16-19, H=7 (8 on FMNH PF9878 and 9880, two Green River specimens), EP=1, UN=3-4, NSPU1=1(0 on several Green River specimens, see Table 5-2), NSPU2=1.

Skull Roof– Although all specimens were preserved in lateral view, with most of the bones in the skull roof displaced and disarticulated, or even crushed, the skull roof can be restored by combining the characters shown on FMNH PF9878, 9880, 9882, 10634, 10639, 10955, 12516 (Fig. 5-2), UALVP17490, 22905, 22917, 31166, 31948, and the holotype.

The nasal on FMNH PF9880, 10634 and UALVP 37128 is somewhat tubular in lateral view and slightly curved. A similar nasal is also preserved on FMNH PF12516 on which it is posteriorly in contact with the frontal.

As in all hiodontiforms, a more or less rectangular mesethmoid, anterior to the frontals (clearly seen on FMNH PF12516), completely separates the left nasal from the right (UALVP 31166 and 22905a).

The frontal is rather well preserved on FMNH PF9878, 10634, and UALVP 22905a and 31166, having an outline identical with that of the Recent *Hiodon*. It is anteriorly slightly narrower than posteriorly with a straight dorso-medial suture margin and a slightly curved lateral (orbital) margin. Its anterior end is interrupted by a deep notch from which the supraorbital canal emerges. This notch appears to fit the posterior end of the nasal (FMNH PF10424). The supraorbital canal on this bone is distributed in the same way as that in the Recent *Hiodon*, medially passing through the frontal along a line parrallel to the orbital edge of the bone. The suture between the two frontals is straight, as in other hiodontiforms; however, the suture between the frontal and the parietal is slightly curved, where the frontal reaches its broadest point.

The parietal on FMNH PF10634 and UALVP 31166 is completely preserved, though it is partly crushed. This bone is posteriorly slightly narrower and somewhat parallelogram-like in shape, with an outline similar to that in †*Yanbiania* (Li, 1987), and a smooth and slightly curved posterior edge. Both the anterior and the posterior margins of this bone are slightly curved anteriorly. Its width is about equal to its length. As in †*Yanbiania*, the postero-ventral corner of the parietal is distinctly projected to form a conical postero-ventral process. The suture between the two parietals is straight, but the suture between the parietal and the frontal is posteriorly arched.

Although the supraoccipital is poorly preserved on all the specimens, an outline of this bone may be drawn from FMNH PF9880, 10634, 10639, 10955, 12516, and UALVP 31166. It is more or less triangular and postero-dorsal to the parietal. As in the Recent *Hiodon*, the supraoccipital seems also to partly separate the posterior parts of the two parietals.

The dermopterotic resembles that in the Recent *Hiodon* (FMNH PF9880), but no details can be discerned from the specimens.

The otic region is either poorly preserved or not exposed on the specimens. It is impossible to give a detailed description of this region. However, it is easy to locate the temporal fenestra on FMNH PF9878 and 9880. These two specimens show a distinct depression bounded by the lateral edge of the parietal, the postero-dorsal edge of the dermopterotic, and the anterior edge of the epiotic. This depression corresponds to the temporal fenestra in other hiodontiforms, appearing to be also covered by a thin extrascapular.

Floor of Neurocranium– This part of the skull is not well exposed; no ventral view of the neurocranium can be seen on any of the specimens. The visible elements forming the floor of the neurocranium are an obitosphenoid that is a subsemicircular bone directly ventral to the frontal (FMNH PF12516) (Fig. 5-2A), a pterosphenoid that is posterior to the obitosphenoid, and a basisphenoid that is ventral to the pterosphenoid (FMNH PF10634 and 12516). These three bones together form the antero-ventral wall of the neurocranium (the dorsal wall of the orbit).

A strong parasphenoid is present, usually bearing five to six pairs of strong conical teeth on the ventral side of its orbital region. It resembles that in the Recent *Hiodon* in both shape and tooth pattern, with conical teeth on the ventral side of the orbital part that are much larger than those ventral to the ascending process. In lateral view this bone runs through the orbit at the level of 1/2 to 2/3 the distance from the top of the orbit (FMNH PF9882, 12516, and UALVP 22905a).

Opercular Series– A complete opercular series is preserved on FMNH PF12516 (Fig. 5-2) and ROM 43220. This series can also be restored by combining the characters shown on ROM 11062, UALVP 15889 (Fig. 5-3A), 15890, 22917, and 31166. Grande (1979) described an opercular series based on SMMP 77.24.1 for †*Eohiodon falcatus*. His description of the opercular series of †*Eohiodon falcatus* is nearly identical with that of †*Eohiodon woodruffi* given by Wilson (1978).

The preopercle on FMNH PF12516 (Fig. 5-2), ROM 11062, 43220, UALVP 15889

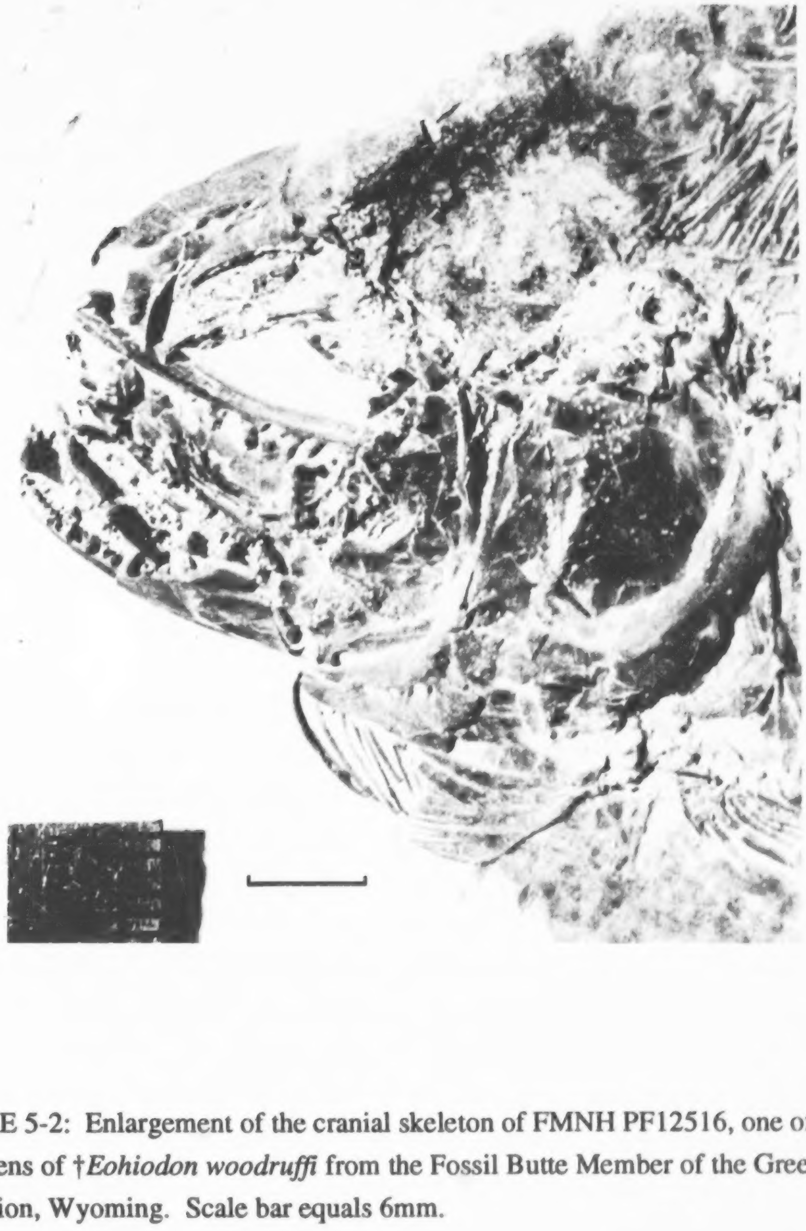

FIGURE 5-2: Enlargement of the cranial skeleton of FMNH PF12516, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming. Scale bar equals 6mm.

(Fig. 5-3A), and 31166 is similar to that in †*Eohiodon rosei* but different from that in the Recent *Hiodon* in having a relatively longer horizontal arm that is only slightly shorter than the vertical arm, with a pointed anterior end that reaches to the level of the posterior edge of the orbit. The vertical and horizontal arms form almost a right angle. The preoperculo-mandibular canal passes through this bone along the orbital margin, giving off at least four branches on the horizontal arm.

The opercle is well preserved on FMNH PF12516, ROM 11062, 43220, and UALVP 15889, and its impression can be seen on UALVP 15890, 22917, and 31166. It is more or less parallelogram-like in shape with a straight anterior edge and slightly excavated dorsal and posterior edges (Fig. 5-3A). The depth is about 1.9 times the width. Unlike that in the Recent *Hiodon*, the postero-dorsal corner of the opercle does not form a sharp projection.

Proportionally the subopercle is less deep than that in the Recent *Hiodon*. The interopercle (UALVP 15889) is similar to that in *Hiodon*.

Circumorbital Region– Although this region is poorly preserved on most of the new specimens from the Horsefly beds, it can be restored by combining the preserved part on UALVP 15889, 31166 (Fig. 5-3B), and 31966. In total, six elements, including the antorbital, can be identified. The antorbital seen on FMNH PF9878, 9882, 10639, and ROM 43220 is somewhat triangular in shape.

In comparison with the Recent *Hiodon* species, the general outline of the infraorbital series is almost identical to that in *Hiodon tergisus*. In total, five infraorbitals are present (Fig. 5-3B). The first infraorbital (UALVP 31166) is elongate but slightly less slender than that in the Recent *Hiodon*. It is immediately ventral to the orbit with its posterior end extending back to the level of the posterior 1/4 of the orbit. The second infraorbital, well preserved on UALVP 15889 and 31166, is more or less oval or suboval in shape, taking a position immediately ventral to the postero-ventral edge of the orbit. The third (io3) and fourth (io4-5) are large plate-like bones that are slightly deeper than long, covering the whole cheek area between the orbit and the preopercle. The fifth infraorbital (=dermosphenotic) that is completely preserved on UALVP 15889 is identical to that in the Recent *Hiodon* in having a tubular and triradiate appearance with the posterior branch to receive the postorbital canal of the cephalic lateral line system.

According to Grande (1979), six infraorbitals (including the dermosphenotic) are present surrounding the orbit of the Green River specimens. However, FMNH PF12516 and ROM 43220 suggest only five, as also seen on the specimens from the Horsefly beds. The first infraorbital lying below the orbit is particularly slender as in the Recent

Hiodon. The 5th infraorbital (=dermosphenotic) on the Green River specimens is also similar to that in the Recent *Hiodon* in shape.

The supraorbital is obviously absent.

Jaws– This region is rather well preserved on FMNH PF9880, UALVP 17492 (Fig. 5-3D) and 22905a. The premaxilla on FMNH PF9880 and UALVP 22905a (Fig. 5-3C) appears to be intermediate between that in †*Eohiodon rosei* and that in *Hiodon* in having a low ascending process or a slightly raised anterior portion. Teeth on this bone are sharp, conical, similar to those on the maxilla in size, and arranged in two rows.

The maxilla seen on FMNH PF9880, 10424, 10634, 10955, ROM 43220, and UALVP 17492, and the impression seen on UALVP 31966a, is tapering and slender anteriorly. It is also comparable with that in the Recent *Hiodon tergisus* in proportions and in having the posterior end extending back to beyond the vertical midline of the orbit (or reaching to the level of the posterior 1/3 of the orbit). Teeth on this bone are sharp, conical, arranged in a single row. These teeth are similar to those on the middle and posterior part of the dentary in the size.

A supramaxilla is definitely absent.

The lower jaw on FMNH PF9880, 10634, 10955, 12516, ROM 43220, and UALVP 17492 shows an outline identical to that of the Recent *Hiodon*. The dentary on these specimens (also see the impression on UALVP 31966a) is anteriorly tapering and slightly curved with a square anterior end (Fig. 5-3D). As in *Hiodon*, it is posteriorly gradually raised to form a gentle slope and an indistinct coronoid process. The conical teeth on this bone are arranged in at least two rows, of which those on the anterior part or labial row are larger than those on the middle and the posterior part or mesial row. The ventral edge of the dentary is rather straight. The preoperculo-mandibular canal passes through the dentary along the lower part of this bone, giving off four to six branches.

As in Recent *Hiodon*, the angular is fused with the retroarticular to form a compound "angulo-retroarticular." Proportionally this compound bone is larger than that in *Hiodon*, with its anterior end inserting in the mesial side of the dentary from its posterior notch. The posterior end of the retroarticular part of the angulo-retroarticular bone is distinctly raised to form a postarticular process (Nelson, 1973). Mesial to the angulo-retroarticular nestles the subtriangular articular (FMNH PF12516) that forms the spacious articulation socket for the peg-like head of the quadrate along with the postarticular process of the angulo-retroarticular.

Palatopterygo-quadrate Arch– Although this part of the skull is crushed on most of the specimens, it still suggests that †*Eohiodon woodruffi* has a palatopterygoid arch

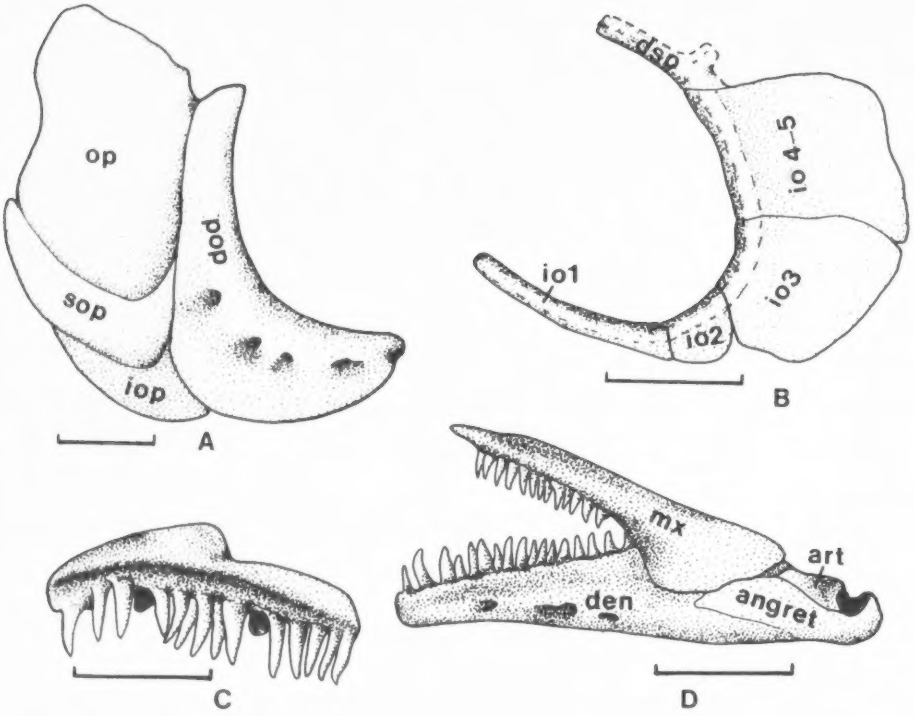
op
pop
sop
iop
A
dsp
io 4–5
io1
io3
io2
B
mx
art
den
angret
C
D

FIGURE 5-3: Some of the cranial skeleton of †*Eohiodon woodruffi*. **A**, opercular series, drawn from UALVP 15889a; **B**, infraorbital series, based on UALVP 31166; **C**, premaxilla, drawn from UALVP 22905; and **D**, lower and upper jaws, from UALVP 17492. Scale bars for **A**, **B**, and **D** equal 5mm; for **C** 2mm.

similar to that in the Recent *Hiodon*. The palatine, which is more or less displaced antero-ventral to the maxilla, and the ectopterygoid, which is postero-dorsal to the maxilla on UALVP 17492, are exactly the same as in the Recent *Hiodon* in shape and tooth pattern. This is further confirmed by the somewhat deformed palatine and ectopterygoid on FMNH PF9880.

The endopterygoid is crushed on all specimens. This bone (FMNH PF9880, UALVP 31948) appears to be also similar to that of *Hiodon*.

The metapterygoid preserved on FMNH PF10734 and 12516 (and its impression that is dorsal to the quadrate on UALVP 15889 and 31996) suggests that this bone is hardly distinguishable from that of *Hiodon* in having a broad subsemicircular outline and a similar position relative to the quadrate.

The quadrate or its impression can be seen on FMNH PF9882, 10634, 12516, ROM 43220, UALVP 15889, 22917, 31166, and 31966. It is similar to that in other hiodontids in having a large articulation head, a fan-like anterior wing, and a leaf-shaped posterior ramus. In detail, this bone slightly differs from that of *Hiodon* but resembles that of †*Eohiodon* in having a relatively deep notch between the anterior wing and the posterior ramus. This notch fits the tapering lower end of the leaf-shaped symplectic.

Hyoid Arch– Although this region is not well exposed on most of the specimens, a nearly complete hyomandibular on UALVP 24135 (Fig. 5-4A) and its outline on FMNH PF9880, 9882, 10634, 12516, and ROM 43220 suggest that it is basically the same as that in †*Eohiodon rosei* in having three strong and equal-sized heads, of which the two dorsal ones articulate with the neurocranium, and the posterior one joins with the opercle. It is also vertically ridged with the ventral end connecting with the symplectic.

A well-preserved ceratohyal or its impression is seen on FMNH PF9880, 10955, UALVP 15889, 15890, and 22905. It is indistinguishable from that of *Hiodon* in having the shape of an hourglass in lateral view.

Although the hypohyal and basihyal are difficult to be seen on all of the specimens, the basihyal tooth plate is well exposed on UALVP 15890 and 22905. This tooth plate is similar to that of *Hiodon* and †*Yanbiania* in shape and tooth pattern, with large conical teeth on its margin and relatively smaller conical teeth on its central part.

UALVP 15889 preserves a complete set of branchiostegals that consists of 10 curved rays of which the first to six are slender, and the others are elongate and lamina. In total, eight to ten (mainly eight on most specimens) branchiostegals are present, as in the Recent *Hiodon* species.

Cephalic Lateral Line System– The cephalic lateral line shown on ROM 43220 has

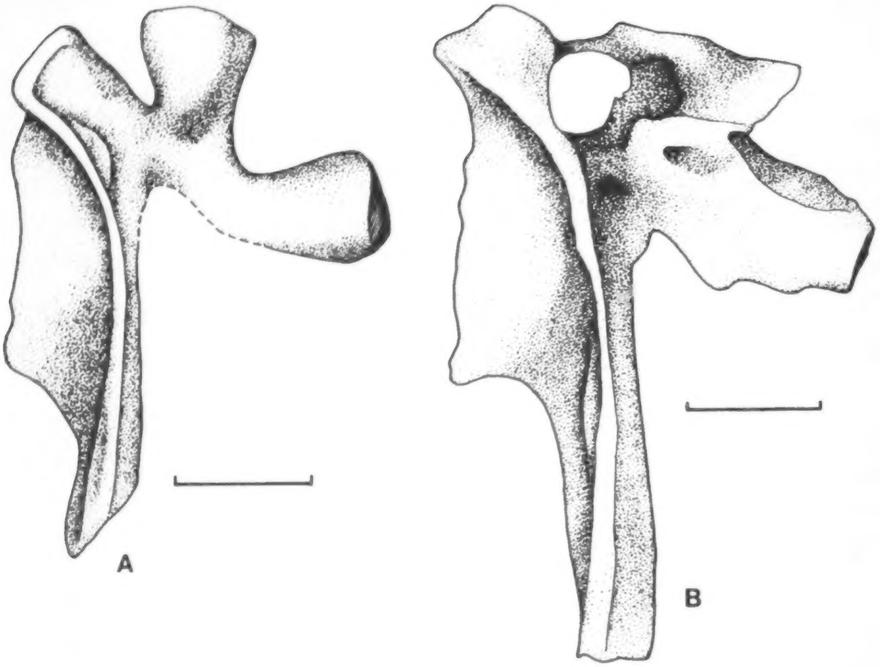

FIGURE 5-4: Hyomandibular of †*Eohiodon* and *Hiodon*. **A**, †*Eohiodon*, based on UALVP 24135. **B**, *Hiodon*, drawn from UALVP 6714. Scale bar for **A** equals 2mm, and for **B** 5mm.

in the same pattern as in *Hiodon*. The supraorbital canal runs through the frontal within a closed tube and ends posteriorly only in the frontal. The infraorbital canal passes through the five infraorbitals within a tube extending along the orbital margin of each of the infraorbitals. Both the infra- and the supraorbital canals start from branches embedded in the triradiate dermosphenotic, in which they join with the postorbital canal that is mainly embedded in the dermopterotic. The preoperculo-mandibular canal gives off at least four branches on the horizontal arm of the preopercle (FMNH PF12516) and five to six in the lower jaw (FMNH PF9880 and 10634).

Vertebral Column and Intermuscular Bones– The vertebral column is nearly completely preserved on the holotype. It consists of 48 centra, of which the precaudals and the caudals are equal in number. The vertebral column on the specimens from Horsefly localities may have one or two more centra than that of holotype, with a range from 46-49 in total (Table 5-2). Among the specimens from the Green River Formation, a complete set of vertebrae can be recovered from FMNH PF9878, 9879, 9880, 9882, 10424, 10633, 10634, 10639, 10955, 12516, 13063, 13064, and ROM 43220. All of these specimens have 24 precaudal vertebrae. In total, 49-50 vertebrae comprise the vertebral column of the Green River specimens (Table 5-2). Each of the individual vertebrae is deeper than long and usually has three lateral ridges. There is no diplospondyly in the examined specimens.

In a comparison of †*Eohiodon woodruffi* (Table 5-2)with †*Eohiodon rosei* (Table 5-1), there is an overlap in the number of the total vertebrae between these two species, the later having 44-47 in total.

Slender pleural ribs are present on all but the anteriormost three precaudal vertebrae. These slightly curved and distally tapering pleural ribs articulate with the centra via parapophyses, extending ventrally to the ventral 1/4 of the margin of the body cavity.

As in other hiodontids epipleurals are absent.

As mentioned by Grande (1979), the left and right halves of the neural arches on the precaudal vertebrae are separate, and not fused with the centra, as also are the left and right halves of the slender and distally tapering neural spines on these precaudal centra. All the neural arches on the precaudal vertebrae bear paired epineurals that extend postero-dorsally from the postero-dorsal side of each of the neural arches.

In total, 17 to 19 (18 on holotype) slightly sigmoid supraneurals are present, with their proximal ends alternating with the neural spines of the precaudals anterior to the dorsal fin.

Although the holotype has 24 caudal vertebrae, the caudal vertebral centra on the

Horsefly specimens have a range of 23 to 25, and the Green River specimens 25 to 26 including the two slightly upturned urals that usually bear neither neural arches nor neural spines.

Except for the first preural that may not bear a neural spine (FMNH PF9879, 10634, 12516, 13063, 13064, and ROM 43220), all of the other preural centra bear complete neural spines on their neural arches. Unlike those on the precaudals, both the neural arches and haemal arches appear to have fused with the centra and their spines.

Caudal Skeleton– Besides on the holotype, well-preserved caudal skeletons are seen on FMNH PF9878 (Fig. 5-5), 9882, 10634, 12516 (Fig. 5-6), ROM 43220, UALVP 24135, 22905, 31948, 31960, and 31966. The caudal skeleton is identical with that of the Recent *Hiodon*, consisting of two upturned urals and four to five preurals (Fig. 5-5). Except for FMNH PF9878 and 9880, which both have eight hypurals, all of the other referred new specimens have seven hypurals that decrease in both length and depth from the first to the seventh. Each of the hypurals is proximally constricted to form a distinct articulation head. The two strong lower hypurals (h1 and h2) articulate but do not fuse with the first ural; they support the lower lobe of the caudal fin along with the strongly ridged parhypural of the first preural centrum and the lengthened haemal spines on the second to the fourth or fifth preurals. Regarding the five or six upper hypurals, only h3 to h4 or h5 directly articulate with the second ural centrum that is somewhat conical in shape. The upper hypurals dorsally decrease in both length and depth, and support the nine principal caudal fin rays in the upper lobe.

Three to four uroneurals are present dorsal to the two upturned urals and the first two preurals; the first extends anteriorly to the posterior end of the third preural, the second to the anterior end of the first preural, and the third to the anterior end of the first ural (FMNH PF12516).

As in all the other hiodontids, there is also only one stick-like epural lying in the space between the first uroneural and the lengthened neural spine of the first preural. This single epural and the three or four uroneurals, with the lengthened neural spines of the first to fourth preurals, support the upper procurrent caudal rays.

The neural spine on the first ural centrum is absent on most specimens. However, a rudimentary (incomplete) neural spine or neural arch may be rarely seen on very few specimens such as FMNH PF9878 (Fig. 5-5), UALVP 31960 and 31966.

All the specimens have only a single neural spine on the second preural, being different from some of the Recent *Hiodon* specimens that may have double neural spines on the second preural (see Table 5-3).

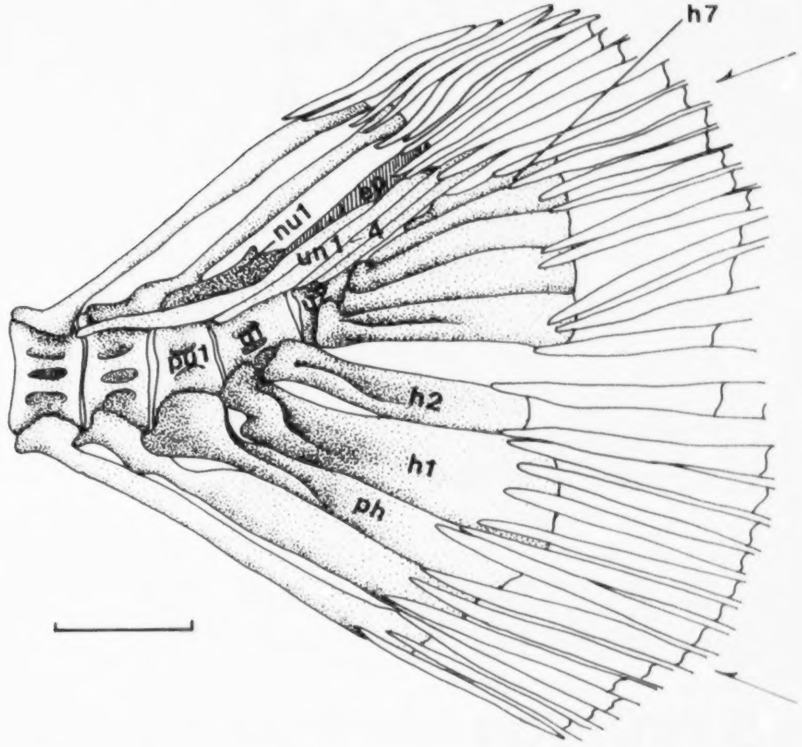
h7
ep
nu1
un1
4
pu1
h2
h1
ph

FIGURE 5-5: Caudal skeleton of FMNH PF9878, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming. Scale bar equals 2mm.

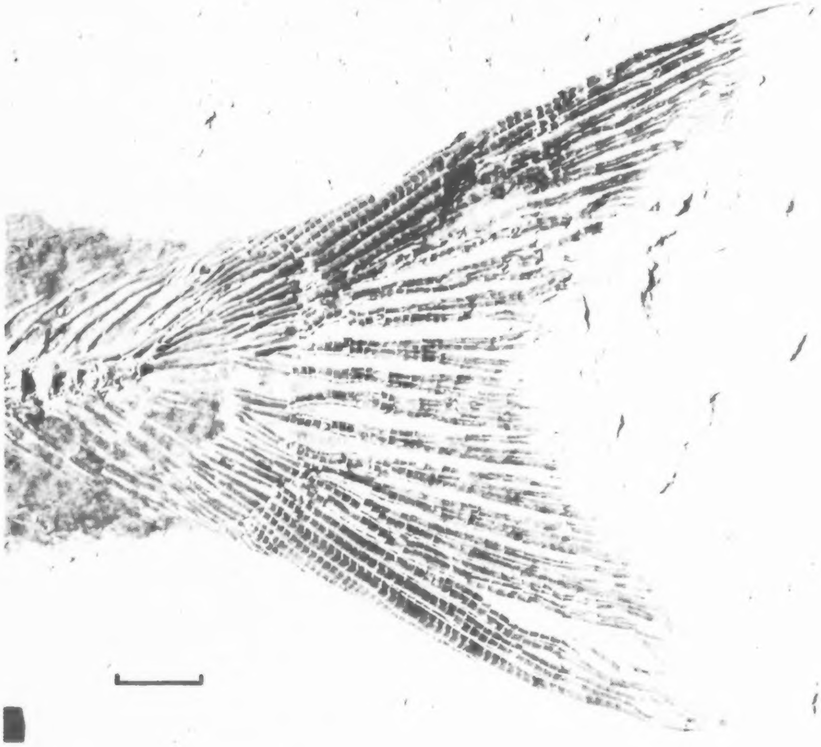

FIGURE 5-6: Photograph of the caudal skeleton of FMNH PF12516, one of the new specimens of †*Eohiodon woodruffi* from the Fossil Butte Member of the Green River Formation, Wyoming. Scale bar equals 5mm.

Pectoral Girdle and Fin– As the main element of the pectoral girdle, a well-preserved cleithrum is seen on FMNH PF9880, 10634, 12516, and ROM 43220, and UALVP 24135. It is sickle-shaped and similar to that in other hiodontids in having a curved and ridged external surface. The only difference is that the angle formed by the vertical dorsal part and the horizontal ventral part is slightly greater than 90° in this Eocene hiodontid fish.

The blade-like supracleithrum (ROM 43220, UALVP 22905) and the angular posttemporal, which has a slender dorsal branch three times as long as the ventral branch (ROM 43220, UALVP 17492), are almost identical with the same elements in the Recent *Hiodon* in shape and proportion.

A small postcleithrum is exposed fully on FMNH PF9880, where it appears to be also similar to that of *Hiodon*.

The corocoid and scapular are not exposed.

The pectoral fins are located at the same position as are those in the Recent *Hiodon*. Each of them has 12-13 rays, of which the first one is distally segmented but unbranched, and the rest are distally both segmented and branched (UALVP 13227, the holotype). The distal tip of the first pectoral fin ray may extend posteriorly to beyond the anterior end of the innominate.

Pelvic Girdle and Fin– As in other hiodontids, the pelvic girdle is formed by two proximally tapering innominates that support the small pelvic fins.

All of the pelvic fins on the referred specimens consist of seven distally segmented and branched rays, as in other hiodontid species. The distance between the origins of the pectoral and pelvic fins is greater than that between the pelvic and anal fins.

Dorsal and Anal fins– In lateral view, the dorsal fin is falcate in outline with a concave posterior margin. It originates anterior to the origin of the anal fin by four to six vertebrae, ending above the 1/2 to posterior 1/3 of the anal fin. In total, 12-15 principal dorsal rays are present on the Horsefly specimens, and 12-14 (mainly 14) on the Green River specimens. The first ray is distally segmented but unbranched, the others are distally both segmented and branched, and the last is double. Proximally, the dorsal fin is supported by 14-16 (15-17 on Green River specimens) dorsal pterygiophores, of which the anteriormost inserting four to six vertebrae anterior to the anteriormost anal pterygiophore.

As in the Recent *Hiodon*, the anal fin is much larger than the dorsal fin with a base length approximately 1.5 times the base length of the dorsal fin (e.g., FMNH PF9882). In total, 16-21 (21-24 on Green River specimens) principal anal fin rays are present; the first is distally segmented but unbranched, the others are distally both segmented and branched, and the last is double. The fin is proximally supported by 17-21 (21- 25 on Green River specimens) proximally tapering anal pterygiophores that decrease in length from the anterior one to the posterior one.

In shape, the anal fin is sexually dimorphic, in that it is anteriorly rounded in presumed males, in which the first nine to ten principal anal rays are much thicker and longer than the rest. In presumed females the anal fin is subtriangular and falcate; the anterior principal anal rays are not thicker than the posterior ones; they gradually decrease posteriorly in length. According to the sexually dimorphic anal fin on the specimens studied for this chapter, I am able to discern five males, of which three are completely preserved (FMNH PF10424, 10639, and UALVP 31948) and two are incomplete (FMNH PF10633 and 10638,). The SL of these presumed males ranges from 98mm to 182mm; while all of the specimens smaller than 98mm SL show no modification in their anal fins. This indicates that individuals in this species mature at a size of about 100mm SL, agreeing with the suggestion of Wilson and Williams (1993).

Caudal Fin– A complete caudal fin, preserved on FMNH PF9878, 9880, 9882, 10424, 10634, 10639, 12516, ROM 43220, UALVP 13227, 24135, 31948, and 31966, is moderately forked. Some 18 principal caudal rays are present on each of the specimens preserved with caudal fin; the dorsal and the ventral marginal principal rays are distally segmented but unbranched; the rest are distally both branched and segmented. Both the upper and the lower lobes have nine principal rays and nine to 11 procurrent rays. The lower lobe is supported by the two lower hypurals articulating with the first ural, the parhypural on the first preuralcentrum, and lengthened haemal spines on the second to the fourth or fifth preurals; the upper lobe is supported by five or six upper hypurals, three or four uroneurals, one epural, and the lengthened neural spines on the first to the fourth preural centra.

Scales– The cycloid scales on FMNH PF9882, ROM 43220, UALVP 17490, 17492, 22905, 31948, and 31966 appear to be similar to those in the Recent *Hiodon* in shape and in having mainly basal (anterior) radii and a subapical nucleus (scale focus). The numerous circuli are evenly distributed in following the outline of the scales.

Grande (1979) gave a detailed description of the scales on the Green River specimens. The well-preserved scales on FMNH PF9882 and ROM 43220 confirm Grande's description, as well as providing more precise information on the counting of the scale rows. On the two specimens, eight rows are present above the lateral line (between the origin of the dorsal fin and the vertebral column), and nine rows below the lateral line (between the origin of the pelvic fin and the vertebral column), suggesting that scale rows in †*Eohiodon woodruffi* are one or two more than those in the Recent *Hiodon* species.

DISCUSSION

i. Remarks on North American †*Eohiodon* Species

1: Validity of †*Eohiodon falcatus*– When Wilson's (1978) paper on †*Eohiodon woodruffi* was in press, Grande (1979) described †*Eohiodon falcatus* based on three specimens from the Green River Formation of Wyoming. At that time, the lack of information on †*Eohiodon woodruffi* made it impossible for Grande to carry out a detailed comparison between his and Wilson's species.

My examination of the new materials referred to as †*Eohiodon woodruffi* and †*Eohiodon falcatus* indicates that these two species are indistinguishable one from another in the vast majority of characters, particularly in the preserved cranial skeletal features (see the above description in detail). The falcate median fins in †*Eohiodon falcatus* are not so much different from those in †*Eohiodon woodruffi*. In addition, the mature size in SL in both †*Eohiodon falcatus* and †*Eohiodon woodruffi* is about the same (at ~100mm SL) in terms of the occurrence of the sexually dimorphic anal fin.

In fact, there are only two meristic differences between these two species: (1) principal anal fin rays in †*Eohiodon falcatus* may be 1-4 more than in †*Eohiodon woodruffi*, and (2) †*Eohiodon falcatus* may have 1-4 more anal pterygiophores than †*Eohiodon woodruffi*. It seems to me that these are not sufficient to be used as the specific diagnosis of †*Eohiodon falcatus*. My recent study suggests that the enlargement of the anal fin in Hiodontiformes *sensu stricto* is proportional to the increase in number of vertebral centra (see Chapter 6). As shown in Table 5-2, both †*Eohiodon falcatus* and †*Eohiodon woodruffi* have a vertebral column consisting of mainly 49 centra. This may imply that they are still at the same level in the lineage of Hiodontiformes *sensu stricto*. According to the consistency in the skeletal system of these two species, †*Eohiodon falcatus* is tentatively considered to be a junior synonym of †*Eohiodon woodruffi*.

2: Comparison Among †*Eohiodon woodruffi*, †*E. rosei*, and the Two Extant *Hiodon* Species– Wilson (1978) made a preliminary comparison mainly in meristics among †*Eohiodon woodruffi*, †*E. rosei*, and the two Recent *Hiodon* species. Grande (1979) noticed some of the morphological differences and similarities among his

†*Eohiodon falcatus*, †*E. rosei*, and the Recent *Hiodon* species. My study confirms that †*Eohiodon woodruffi* resembles †*E. rosei* but differs from the two Recent *Hiodon* species in having fewer total vertebrae, fewer principal anal rays, fewer anal pterygiophores, more principal dorsal fin rays, and more dorsal pterygiophores (Tables 5-1 and 5-2).

It is notable that †*Eohiodon woodruffi* and †*E. rosei* closely resemble the two Recent *Hiodon* species in osteology (Cavender, 1966; Wilson, 1977, 1978, Grande, 1979). Their caudal skeleton is exactly the same as that in the two Recent *Hiodon* species (Fig. 5-5), and their cranial skeletal characters are also basically similar to those of *Hiodon*. The only important differences are: (1) the horizontal arm of the preopercle is proportionally relatively longer in †*Eohiodon woodruffi* and †*E. rosei* than in the two Recent *Hiodon* species; (2) †*Eohiodon woodruffi* and †*E. rosei* have a more or less parallelogram-like opercle that does not have a distinct sharp postero-dorsal projection, while the opercle in the two Recent *Hiodon* species is strongly excavated both posteriorly and dorsally with a distinct postero-dorsal projection; (3) the upper part of the hyomandibular consists of three equal-sized heads (including the opercular process) in †*Eohiodon woodruffi* and †*E. rosei* (a typical †*Eohiodon* feature), while in the two Recent *Hiodon* species the dorsal end of the hyomandibular is bridged (a typical *Hiodon* feature).

As regards the lower and upper jaws, †*Eohiodon woodruffi* appears to be intermediate between †*E. rosei* and the two Recent *Hiodon* species. The premaxilla in †*Eohiodon rosei* is similar to that in lycopteriforms and other hiodontiforms, such as †*Yanbiania* (Li, 1987), in having a raised anterior portion. In *Hiodon* it is, however, anteriorly as deep as or even slightly shallower than posteriorly. †*Eohiodon woodruffi* has a premaxilla that has a lower ascending process or only a slightly raised anterior portion.

A distinct feature of the premaxilla in *Hiodon* is that it bears a mid-dorsal concavity. The two †*Eohiodon* species do not share this character state with *Hiodon*.

In the pattern of the jaws and infraorbital series, †*Eohiodon woodruffi* is more similar to *Hiodon tergisus* than it is to †*E. rosei* and *Hiodon alosoides*. As in *Hiodon tergisus*, the posterior end of the maxilla in †*Eohiodon woodruffi* extends back to beyond the vertical midline of the orbit, usually reaching to the level of the posterior 1/3 of the orbit. Correspondingly, the mouth corner in †*Eohiodon woodruffi* is located at a level near the vertical midline of the orbit. The general outline of the infraorbital series of †*Eohiodon woodruffi* (Fig. 5-3B) is basically the same as that of the Recent *Hiodon*

TABLE 5-1: Meristics of †*Eohiodon rosei.*

	PCV	CV	TV	BR	PFR	VFR	DFR	DP	AFR	AP	CFR	H	EP	SPN	NSPU1	NSPU2	UN
CMN 2156*	22	24	46	9	13	7	13	14	15	16	18	7	1	18	0	1	3
ROM 11101	?	?	?	?	?	?	13	?	?	17	18	7	1	?	?	?	3
ROM 11138	22	22	44	7	12	7	11	13	15	16	18	7	1	?	1	1	3
UALVP 12221	22	25	47	9	10	7	12	?14	?	18	?	?	?	?	?	?	?
UALVP 22915	23	24	47	10	13	7	12	14	16	17	19	7	1	17	1	1	3
UALVP 27113	?	?	?	?	?	?	?	?	18	18	18	7	1	?	?	?	2
UALVP 27119	?	24	?	?	10	7	11	14	17	17	18	7	1	?	1	1	3
UALVP 27122	23	24	47	?	11	7	12	14	18	18	18	7	1	16	1	1	2
ROM 11026	?	23	?	9	?	7	13	14	16	17	18	7	1	?	1	1	3
AVERAGE	22	24	46	9	13	7	13	14	16	17	18	7	1	18	1	1	3

TABLE 5-2: Meristics of †*E. woodruffi*. Specimens labelled as FMNH, ROM, and UMVP were referred to as †*E. falcatus*.

	PCV	CV	TV	BR	PFR	VFR	DFR	DP	AFR	AP	CFR	H	EP	SPN	NSPU1	NSPU2	UN
†E.woodruffi	22-24	24-25	46-49	9	12~13	7	12~15	15	18-19	19-20	18	7	?	?	?	?	?
UALVP 13227	24	24	48	9	13	7	13	15	18	20	18	7	1	18	1	1	3
UALVP 17492	24	25	49	9	13	7	14	17	20	21	?	?	1	19	1	1	?
UALVP 22905	24	25	49	10	12	7	13	16	17	20	18	7	1	16	1	1	4
UALVP M3	23	23	46	9	13	7	13	14	17	19	18	7	1	17	1	1	3
UALVP 24135	23	23	46	9	13	7	13	14	16	17	18	7	1	?	1	1	4
UALVP 31948	24	25	49	8	13	7	15	16	19	20	18	7	1	?	1	1	3
UALVP 31966	?	?	?	8	12	7	14	?	19	?	18	7	1	?	1	1	3
UMVP 6499*	24	25	49	8	13	7	14	16	23	22	18	7	1	18	1	1	4
FMNH PF9878	24	26	50	?	12	7	14	17	24	23	18	8	1	19	1	1	4
FMNH PF9879	24	26	50	?	?	7	14	16	?	21	18	7	1	18	0	1	4
FMNH PF9880	24	25	49	8	12	7	12	16	21	21	18	8	1	17	1	1	3
FMNH PF9882	24	25	49	8	13	7	14	17	23	22	18	7	1	18	1	1	4
FMNH PF10633	24	26	50	?	12	?	12	15	?	25	18	7	1	17	1	1	3
FMNH PF10634	24	25	49	8	?	7	14	17	22	23	18	7	1	17	0	1	3
FMNH PF10639	24	25	49	?	13	7	14	17	24	24	18	7	1	17	1	1	3
FMNH PF10955	24	25	49	8	12	7	14	17	22	24	18	7	1	17	1	1	4
FMNH PF12516	24	25	49	8	?	7	14	16	24	23	18	7	1	?	0	1	4
FMNH PF13063	24	25	49	?	?	7	13	15	?	23	?	7	1	?	0	1	3
FMNH PF13064	24	26	50	?	12	?	14	16	22	24	18	7	1	17	0	1	3
ROM 43220	24	25	49	8	12	7	14	15	?	?	18	7	1	18	0	1	3
AVERAGE	24	24	48	9	13	7	13	15	18	20	18	7	1	18	1	1	3

tergisus, in which the 3rd and 4-5th posterior infraorbitals are deeper than long, forming a relatively shorter cheek region than in *Hiodon alosoides*. These character states shared by †*Eohiodon woodruffi* and *Hiodon tergisus* may imply a close relationship between these two species. Future study is likely to clarify this relationship.

ii. Reassessment of Taxonomic Position of Hiodontidae and Notopteridae

Since Bridge (1900) linked *Hiodon* with *Notopterus* based on the so-called "swim bladder-ear connection," the Hiodontidae have been most often grouped in Notopteroidei with Notopteridae (Regan, 1909; Berg, 1940; Greenwood, 1963, 1970; Greenwood et al., 1966; Cavender, 1966; Patterson and Rosen, 1977; Grande, 1979; Lauder and Liem 1983; Nelson, 1994).

Gosline (1960) had earlier noticed the difficulty in relating hiodontids with notopterids in terms of their skeletal characters. He defined the superfamily Hiodontoidea hierarchically equal to two other groups of Osteoglossiformes (Osteoglossoidea and Notopteroidea). Nevertheless, his superfamily content was the same as the family Hiodontidae, containing only the Recent *Hiodon*. Not long after Gosline, McAllister (1968) denied an association of Hiodontidae with Notopteridae and other osteoglossiform fishes. He promoted Hiodontidae to Hiodontoidei and placed it in his Clupeiformes as a monotypic suborder based on his study of the branchiostegals.

Greenwood (1970) then grouped Hiodontidae and †Lycopteridae in his superfamily Hiodontoidea after he proposed a relationship between *Hiodon* and †*Lycoptera* (Müller, 1847), a primitive teleost from the Upper Jurrassic and Lower Cretaceous of East Asia. He considered his Hiodontoidea to be an apomorphic sister-group of Notopteroidea, and grouped them in the suborder Notopteroidei. A similar opinion was also held by Patterson and Rosen (1977), Grande (1979), Lauder and Liem (1983), and Nelson (1994).

During the last three decades, the content of Hiodontidae and †Lycopteridae has been changed with the discoveries of more new materials and with progress in the study of lycopterids and hiodontids (Zhang and Zhou, 1976; Ma, 1980; Sytchevskaya 1986; Li, 1987). The family Hiodontidae has been shown to contain four valid genera (*Hiodon*, †*Eohiodon*, †*Plesiolycoptera*, and †*Yanbiania*), and Lycopteridae to contain at least two (†*Lycoptera* and †*Tongxinichthys*). My comparison of hiodontids and lycopterids with notopterids, mormyroids, and other well-established osteoglossiform genera suggests that the previously commonly accepted Notopteroidei, containing †Lycopteridae, Hiodontidae, and Notopteridae, is a polyphyletic taxon. This is indicated by the result of a cladistic analysis of 65 characters (see Appendix 5-II) and the distribution of their states in 22 taxa (see Table 5-3A-B).

The cladistic analysis leads to nine shortest trees, all of which suggest the same phylogeny of Hiodontidae in Osteoglossomorpha as that shown in Fig. 5-7 (the preferred tree generated by MacClade 3.04) and Fig. 5-8 (the strict consensus tree generated by PAUP 3.1.1 based on the nine most parsimonious trees). These two cladograms provide a new phylogenetic framework for further discussion of the systematic positions of †Lycopteridae, Hiodontidae, and Notopteridae in the clade Osteoglossomorpha.

1. Stem-group Relationship between †Lycopteridae and Osteoglossomorpha– According to Figs. 5-7 and 5-8, †Lycopteridae is not more closely related to Hiodontidae than it is to other taxa in Osteoglossomorpha. Phylogenetically, this East Asian Late Jurassic-Early Cretaceous teleostean family takes the stem-group position in the clade Osteoglossomorpha. This relationship is supported by four of the six skeletal synapomorphies seen in both fossil and extant osteoglossomorph fishes (see Chapter 7 in detail): (1) single epural (=12[1]), (2) absence of supraorbital (=13[1]), (3) presence of primary bite of mouth between parasphenoid and basihyal (=14[1]), and (4) fewer than 17 principal branched caudal fin rays (=15[1]). Other character states probably suggesting the stem-group relationship between †Lycopteridae and Osteoglossomorpha are the number of pelvic fin rays (maximum 6) (=6[2]) and the oval or kidney-shaped opercle (=20[2]). Further discussion about the stem-group relationship between †Lycopteridae and Osteoglossomorpha will be given in Chapter 7.

As regards the temporal fenestra, it was first noticed by Gaudant (1968) to be present in lycopterids and later used by Greenwood (1970) as one of the most important character states to link †Lycopteridae with Hiodontidae. This fenestra is here considered to be homologous with the "pre-epiotic fossa" (=9[1]) seen in clupeomorphs (Ridewood, 1904; Grande, 1985) because these two structures hold the same position in the skull and are all bordered by the parietal, dermopterotic, and epiotic (they may be covered by the supratemporal in the extant adult specimens). A similar structure is also present in *Pantodon* (Osteoglossidae), *Papyrocranus* (Notopteridae), Osmeridae, and Salmonidae (pers. obs.). It seems to me that this character state is no longer valid in support of the relationship between †Lycopteridae and Hiodontidae because of its homoplasy.

2. Two Different Sister-group Relationships– The swimbladder-ear connection (11[1]), which is traditionally used to link Hiodontidae with Notopteridae, has lost its significance in support of the relationship between the two families. A similar connection between the swimbladder and ears has also been found in mormyroids

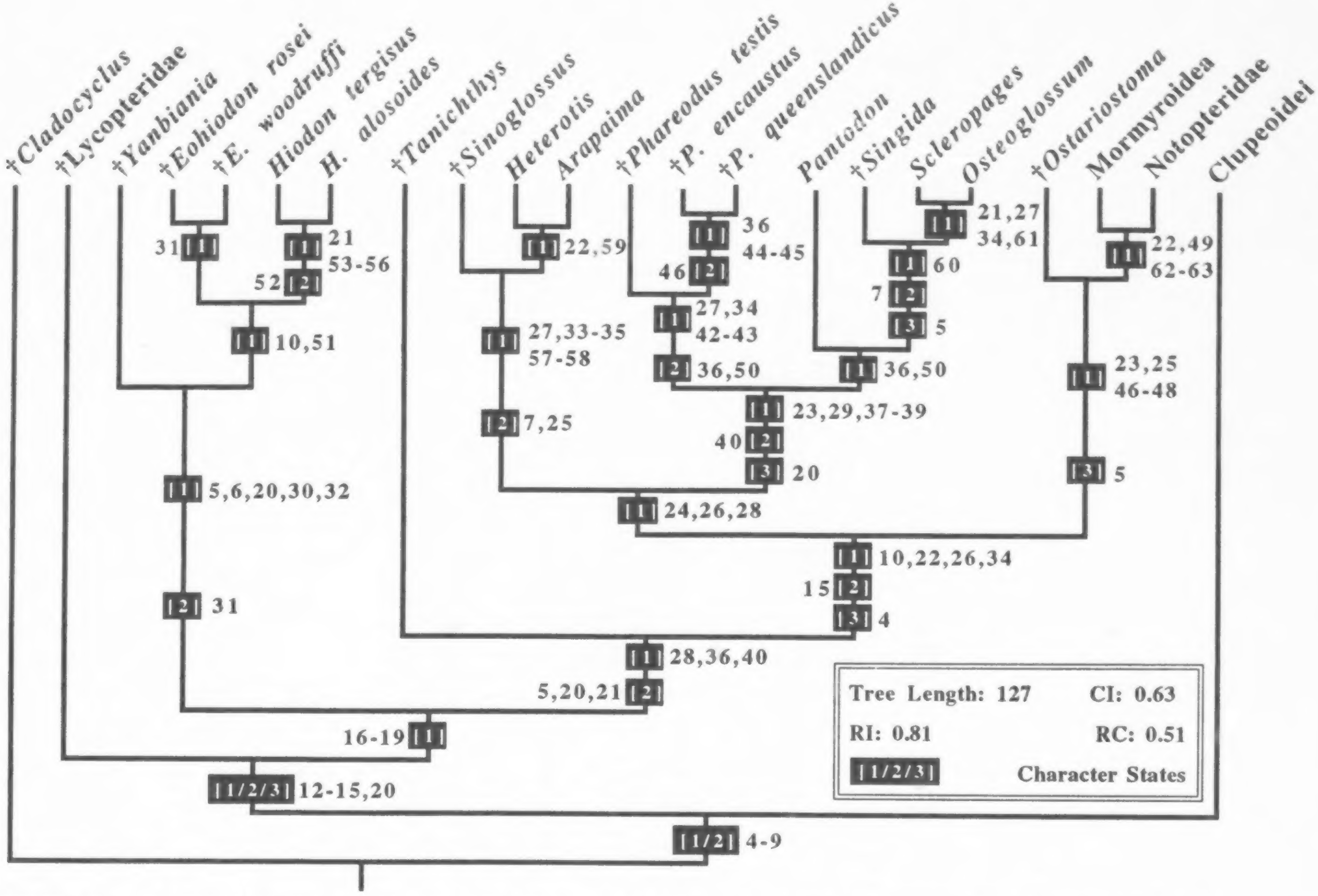
†Cladocyclus
†Lycopteridae
†Yanbiania
†Eohiodon rosei
†E. woodruffi
Hiodon tergisus
H. alosoides
†Tanichthys
†Sinoglossus
Heterotis
Arapaima
†Phareodus testis
†P. encaustus
†P. queenslandicus
Pantodon
†Singida
Scleropages
Osteoglossum
†Ostariostoma
Mormyroidea
Notopteridae
Clupeoidei
31 [1]
[1] 21 53-56
52 [2]
[1] 10,51
[1] 5,6,20,30,32
[2] 31
[1] 22,59
[1] 27,33-35 57-58
[2] 7,25
[1] 36 44-45
46 [2]
[1] 27,34 42-43
[2] 36,50
[1] 21,27 34,61
[1] 60
7 [2]
[3] 5
[1] 36,50
[1] 23,29,37-39
40 [2]
[3] 20
[1] 24,26,28
[1] 22,49 62-63
[1] 23,25 46-48
[3] 5
[1] 10,22,26,34
15 [2]
[3] 4
[1] 28,36,40
5,20,21 [2]
16-19 [1]
[1/2/3] 12-15,20
[1/2] 4-9
Tree Length: 127
CI: 0.63
RI: 0.81
RC: 0.51
[1/2/3] Character States

FIGURE 5-7: Preferred shortest tree showing the phylogeny of Hiodontidae and Notopteridae in Osteoglossomorpha. Characters and their distribution states are shown in Table 5-3A-B and Appendix 5-I.

(Greenwood, 1973) and some clupeomorphs (see Greenwood, 1973; Grande, 1985).

In addition, I found at least the following nine important differences that do not support the relationship between Hiodontidae and Notopteridae.

1). The nasals in all of the notopterids contact each other above the mesethmoid (Ridewood, 1904; Gregory, 1933; Greenwood, 1963; Taverne, 1978; and pers. obs.), but are separated by the mesethmoid in Hiodontidae.

2). The cephalic lateral line canal system has no pore opening to the outside in notopterids (Lauder et al., 1983). In Hiodontidae, there are pores opening directly to the outside (Ridewood, 1904; Greenwood, 1970; Nelson, 1972a; Taverne, 1978; Li, 1987).

3). The subopercle is absent in notopterids (Ridewood, 1904; Greenwood et al., 1966; Taverne, 1978, and pers. obs.), but it is developed in all hiodontids (see Cavender, 1966; Greenwood, 1970; Wilson, 1978; Grande, 1979; Li, 1987).

4). In notopterids, the pelvic fins have degenerated or even disappeared, and the anal fin and the caudal fin have been merged into one. However, the pelvic fins in Hiodontidae are developed, and the anal fin is completely separated from the caudal fin.

5). The caudal fin is evidently reduced or even invisible in notopterids (Whitehouse, 1910; Greenwood et al., 1966; Taverne, 1978; pers. obs.); it is, however, developed in Hiodontidae, appearing to be homocercal and forked with 16 branched principle rays supported by 7 hypurals, 3-4 uroneurals, and one epural.

6). Abdominal scutes superficially resembling those in Clupeomorpha are present in both fossil and Recent notopterids (see Sanders, 1934; Taverne, 1978; Grande, 1985). These abdominal scutes are, however, definitely absent in all of the hiodontid species.

7). As in clupeomorphs (Patterson, 1970; Patterson and Rosen, 1977), all of the notopterids have a supratemporal commissural sensory canal passing through the parietals (Taverne, 1978; Grande, 1985; pers. obs.). This feature is also seen in fossil †*Phareodus* and the Recent *Osteoglossum* and *Scleropages* (Grande, 1985; pers. obs.). In the Recent *Hiodon* species (possible also in fossil hiodontids), the supratemporal commissural sensory canal (=commissure sensorielle extrascapulaire, Taverne, 1977), if present, passes through only the supratemporal.

8). In the inner ear of *Notopterus*, the utriculus and semicircular canals are completely separated from the sacculus and the lagena (Lauder et al., 1983, Fig. 23A). These parts, however, are connected in *Hiodon* (Greenwood, 1973: fig. 6, and pers. obs.).

9). There are also differences in soft tissue between *Hiodon* and *Notopterus*. For example, the pyloric caecam turning to the left of the stomach number at least two in

TABLE 5-3A: Data matrix showing the distribution of states of characters 1-33 in Osteoglossomorpha and selected out-groups. Characters, represented by the bold numbers, are listed in the appendix.

TAXA CHARACTERS AND THEIR STATES		†*Cladocyclus*	†Lycopteridae	†*Yanbiania*	†*Eohiodon rosei*	†*E. woodruffi*	*Hiodon tergisus*	*H. alosoides*	†*Tanichthys*	†*Sinoglossus*	*Heterotis*	*Arapaima*	†*Phareodus testis*	†*P. encaustus*	†*P. queenslandicus*	*Pantodon*	†*Singida*	*Scleropages*	*Osteoglossum*	†*Ostariostoma*	Mormyroidea	Notopteridae	Clupeoidei
1	Lpu2	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1
2	Ud	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3	Dcs	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4	Un	0	1	1	1	1	1	1	1	?	3	3	3	3	3	3	2	3	3	2	3	3	1
5	#H	0	1	1	1	1	1	1	2	?	2	2	2	2	?	2	3	2	3	3	3	3	2
6	Vfr	0	2	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
7	Nana	0	1	1	1	1	1	1	1	2	2	2	1	1	1	1	2	2	2	1	1	2	1
8	Bp	0	1	1	1	1	1	1	?	?	0	0	0	0	0	0	0	0	0	1	1	1	1
9	Pe-f	0	1	1	1	1	1	1	0	?	0	0	0	0	0	1	0	0	0	0	0	0	1
10	So.c	0	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11	S-ec	?	?	?	?	?	1	1	?	?	0	0	?	?	?	0	?	0	0	?	1	1	1
12	Ep	0	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	2	0
13	So	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
14	Pbm	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
15	Cfr	0	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	1	2	0
16	Smx	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
17	Io4-5	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0
18	Tbhb	?	?	?	?	?	1	1	?	?	1	1	?	?	?	1	?	1	1	?	1	1	0
19	Int	?	?	?	?	?	1	1	?	?	1	1	?	?	?	1	?	1	1	?	1	1	0
20	Op	0	2	1	1	1	1	1	2	2	2	2	3	3	3	3	3	3	3	0	0	4	0
21	Na	0	0	0	0	0	1	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	0
22	U2-h	0	0	0	0	0	0	0	0	?	1	1	0	0	0	1	0	1	1	0	1	1	0
23	Pomc	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0
24	Nu1	0	0	0	0	0	0	0	0	?	1	1	2	2	?	1	1	1	1	0	0	1	0
25	Io2	0	0	0	0	0	0	0	2	2	2	2	0	0	?	0	0	0	0	1	1	1	0
26	Dsh	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1	0
27	Prda	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	0	0	1	0
28	P-qa	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
29	Paec	0	0	0	0	0	0	0	0	?	0	1	1	1	1	1	?	1	1	0	0	1	0
30	Dapt	0	0	1	1	1	1	1	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0
31	Hmh	0	0	2	1	1	2	2	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0
32	Sdsp	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
33	CKW	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0

TABLE 5-3B: Data matrix showing the distribution of states of characters 34-65 in Osteoglossomorpha and selected out-groups. Characters, represented by the bold numbers, are listed in the appendix.

TAXA / CHARACTERS AND THEIR STATES		*†Cladocyclus*	**†Lycopteridae**	*†Yanbiania*	*†Eohiodon rosei*	*†E. woodruffi*	*Hiodon tergisus*	*H. alosoides*	*†Tanichthys*	*†Sinoglossus*	*Heterotis*	*Arapaima*	*†Phareodus testis*	*†P. encaustus*	*†P. queenslandicus*	*Pantodon*	*†Singida*	*Scleropages*	*Osteoglossum*	*†Ostariostoma*	**Mormyroidea**	**Notopteridae**	**Clupeoidei**
34	Sca	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	1	1	0	1	0	0
35	Lvap	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	0	0
36	Hap	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	1	1	0	0	0	0
37	Bhbb	0	0	0	0	0	0	0	?	?	0	0	1	1	?	1	?	1	1	?	1	0	0
38	Pena	0	0	0	0	0	0	0	?	0	0	0	1	1	1	1	1	1	1	1	0	0	0
39	Pfr1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0
40	Ja	0	0	0	0	0	0	0	1	0	0	0	1	2	2	2	2	2	2	0	0	0	0
41	Fr	0	0	0	0	0	0	0	0	0	0	0	2	2	2	0	0	0	0	0	0	0	0
42	Rdwo	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
43	Ses	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
44	Pop	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
45	Hm	0	0	0	0	0	0	0	0	?	0	0	0	1	1	0	0	0	0	0	0	0	0
46	Sio3	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	1	1	1	0
47	IOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
48	Ioc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
49	Utr	?	?	?	?	?	0	0	?	?	0	0	?	?	?	0	?	0	0	?	1	1	0
50	Mc	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1	0	0	1
51	Ash	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
52	Pmx	0	0	0	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
53	Pdpo	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
54	Mcpm	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
55	Npu1	0	0	0	0	0	1	1	0	?	0	0	0	0	?	0	0	0	0	0	0	0	0
56	#Pu2	1	0	0	0	0	1	1	0	?	0	0	1	1	?	0	0	0	0	0	0	0	0
57	Pemx	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
58	Aio1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
59	Bhtp	0	0	0	0	0	0	0	0	?	1	1	0	0	?	0	?	?	?	?	?	?	?
60	Pmop	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
61	Osh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
62	Scsc	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	1	1
63	Mdc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
64	Sop	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
65	Abs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

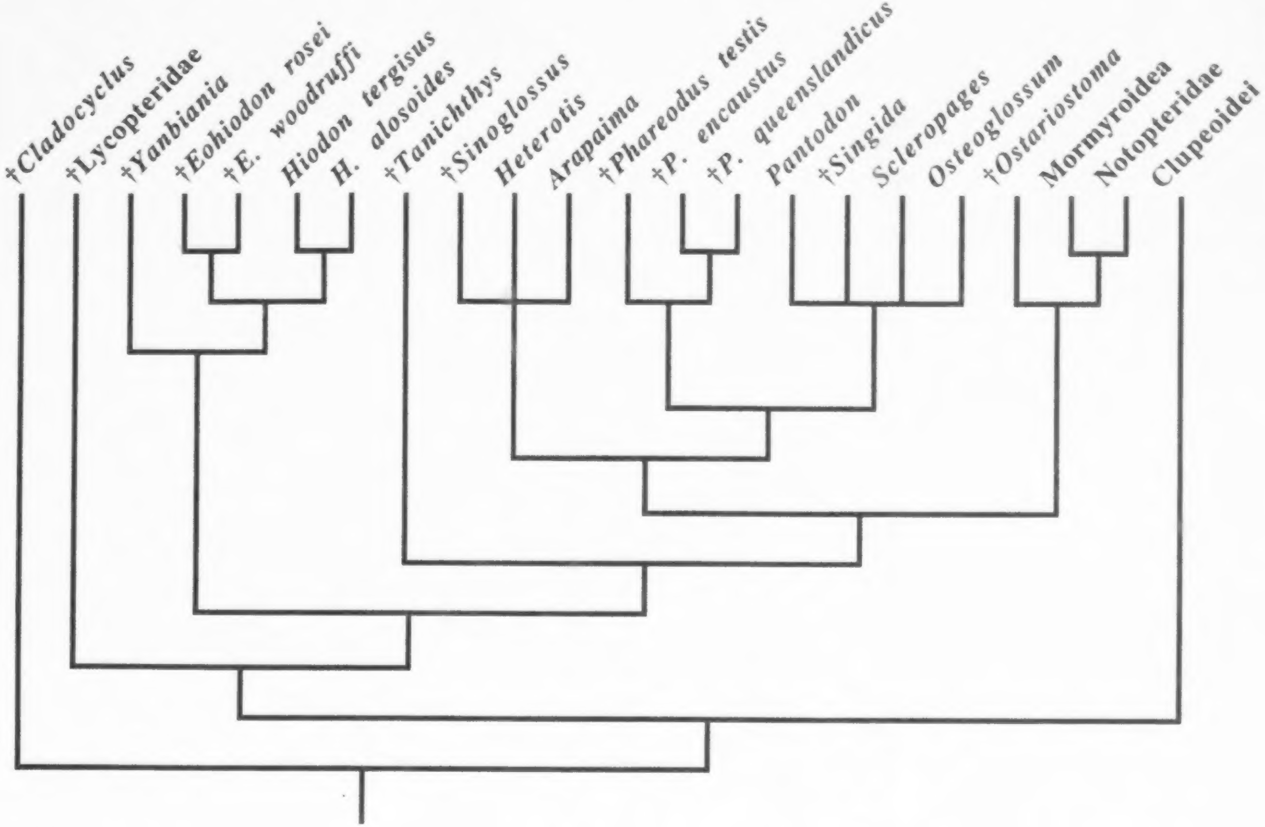
†Cladocyclus
†Lycopteridae
†Yanbiania
†Eohiodon rosei
†E. woodruffi
Hiodon tergisus
H. alosoides
†Tanichthys
†Sinoglossus
Heterotis
Arapaima
†Phareodus testis
†P. encaustus
†P. queenslandicus
Pantodon
†Singida
Scleropages
Osteoglossum
†Ostariostoma
Mormyroidea
Notopteridae
Clupeoidei

FIGURE 5-8: Strict consensus tree generated by PAUP 3.1.1 based on nine most parsimonious trees. Note that the Hiodontidae and Notopteridae take the same phylogenetic position as that shown in Fig. 5-8, the preferred tree produced by MacClade 3.04.

Notopterus, but never more than one in *Hiodon* (Nelson, 1972b).

As shown in Figs. 5-7 and 5-8, my study recognizes two different sister-group relationships among hiodontids and notopterids. The first is between the Hiodontidae (Hiodontiformes *sensus stricto*) and the Osteoglossiformes. This relationship is strongly supported by the six skeletal synapomorphies shared by these two clade: 12[1], single epural; 13[1], absence of supraorbital; 14[1], presence of primary bite of mouth between parasphenoid and basihyal; 15[1], fewer than 17 principal branched caudal fin rays; 16[1], absence of supramaxilla; and 17[1], io4 fused with io5. In addition, the two extant North American *Hiodon* species also share the two soft tissue character states with all the other Recent osteoglossomorphs distributed in the southern continents: 18[1], paired tendon bones on 2nd hypobranchial or 2nd hypobranchial and basibranchial; and 19[1], intestine coiling to the left of the esophagus and stomach. These synapomorphies define the monophyly of the clade of Osteoglossomorpha containing Hiodontidae (Hiodontiformes *sensus stricto*) and Osteoglossiformes (also see Chapter 7 for details).

The second sister-group consists of Notopteridae and Mormyroidea. These two taxa form a monophyletic group (Notopteroidei) which is defined by five synapomorphies: (1) five or fewer hypurals (5[3]), (2) io2 more or less rectangular and moderate in size (25[1]), (3) io3 irregularly rectangular (46[1]), (4) presence of an infraorbital ledge formed by lateral extention of orbital margin of io1 and io2 (47[1]), and (5) infraorbital canal on io1 to io3 open in a groove (48[1]). For the extant species, the monophyly of Notopteroidei is also defined by 49[1] (utriculus completely separated from sacculus and lagena) and 63[1] (mandibular canal open in a groove parallel to ventral edge of dentary).

Further investigation suggest that Notopteroidei are most closely related to Osteoglossoidei. These two taxa form the clade Osteoglossiformes based on eight synapomorphies: (1) decrease of uroneurals to one or zero (4[3]), (2) 15 or fewer principal branched caudal fin rays (15[2]), (3) nasal gutter-like or irregularly subrectangular (21[2]), (4) upper hypurals fused with u2 (22[1], (5) u1 bearing at least one completely developed neural spine (24[1]), (6) dorsal fin rounded in shape (26[1]), (7) posterior rays of dorsal and anal fins longer than or nearly as long as anterior ones (27[1]), and (8) palatine and ectopterygoid fused to form palato-ectopterygoid (29[1]).

CONCLUSIONS

1. The two meristic differences between †*Eohiodon woodruffi* and †*E. falcatus* (both principal anal fin rays and anal pterygiophores in †*Eohiodon falcatus* 1-4 more than in †*Eohiodon woodruffi*) are not sufficient to define †*Eohiodon falcatus*. The consistency in the skeletal system of these two species strongly suggests that †*Eohiodon falcatus* is a junior synonym of †*Eohiodon woodruffi*.

2. Meristically, †*Eohiodon woodruffi* resembles †*E. rosei* but differs from the two Recent *Hiodon* species in having fewer total vertebrae, fewer principal anal rays, fewer anal pterygiophores, more principal dorsal fin rays, and more dorsal pterygiophores.

3. †*Eohiodon rosei* and †*E. woodruffi* are hardly distinguishable from the two Recent *Hiodon* species, having exactly the same morphology of the caudal skeleton. Their cranial skeleton differs from that of *Hiodon* species mainly in three features: (1) the horizontal arm of the preopercle is proportionally longer in †*Eohiodon rosei* and †*E. woodruffi* than in the two Recent *Hiodon* species; (2) the opercle in †*Eohiodon rosei* and †*E. woodruffi* is parallelogram-like in shape, while the opercle in *Hiodon* species is strongly excavated both posteriorly and dorsally with a distinct conical postero-dorsal projection; (3) the upper part of the hyomandibula consists of three equal-sized heads (including the opercular process) in †*Eohiodon rosei* and †*E. woodruffi* , while in *Hiodon* species the dorsal end of the hyomandibula is bridged.

4. The traditionally accepted Notopteroidei, containing †Lycopteridae, Hiodontidae, and Notopteridae, is a polypheletic group. In fact, †Lycopteridae is not more closely related to Hiodontidae than it is to other taxa in the clade of Osteoglossomorpha. This fossil family takes the stem-group position of Osteoglossomorpha. Hiodontidae (Hiodontiformes *sensus stricto*) is the sister-group of Osteoglossiformes. Species in this family are not more closely related to notopterids than they are to other taxa in Osteoglossiformes. Notopteridae is most closely related with Mormyroidea; together they form the sister-group of the clade Osteoglossoidei.

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APPENDIX 5-I

65 characters used in cladistic analysis

1. Length of neural spine on Pu2: (Lpu2)
   [0] = shorter than neural spine on Pu3
   [1] = as long as neural spine on Pu3

2. Urodermals: (Ud)
   [0] = present
   [1] = absent

3. Upper caudal scutes: (Dcs)
   [0] = present
   [1] = absent

4. Uroneurals: (Un)
   [0] = more than four
   [1] = three to four
   [2] = one or two
   [3] = absent

5. Number of hypurals: (#H)
   [0] = more than seven
   [1] = seven
   [2] = six
   [3] = five or fewer

6. Pelvic fin rays (when present): (Vfr)
   [0] = more than seven
   [1] = seven
   [2] = six or fewer

7. Relationship between two nasals: (Nana)
   [0] = separated by anterior portion of frontal
   [1] = separated mainly by mesethmoid
   [2] = meeting with each other

8. Basipterygoid process: (Bp)
   [0] = present
   [1] = absent

9. Pre-epiotic fossa (=temporal fenestra): (Pe-f)
   [0] = absent
   [1] = present

10. Supraorbital canal: (So.c)
    [0] = ending in parietal
    [1] = ending in frontal

11. Swimbladder-ear connection (directly): (S-ec)
    [0] = absent
    [1] = present

12. Epural: (Ep)
    [0] = two to three
    [1] = one
    [2] = absent

13. Supraorbital: (So)
    [0] = present
    [1] = absent

14. Primary bite of mouth between parasphenoid and basihyal: (Pbm)
    [0] = absent
    [1] = present

15. Principal branched caudal fin rays: (Cfr)
    [0] = 17 or more
    [1] = 16
    [2] = 15 or fewer

16. Supramaxilla: (Smx)
    [0] = present
    [1] = absent

17. 4th and 5th infraorbitals: (Io4-5)
    [0] = separate from each other
    [1] = fused with each other

18. Paired tendon bones on 2nd hypobranchial or 2nd hypobranchial and basibranchial: (Tbhb)
    [0] = absent
    [1] = present

19. Intestine: (Int)
    [0] = coiling to right of esophagus and stomach
    [1] = coiling to left of esophagus and stomach

20. Opercle: (Op)
    [0] = more or less irregular trapezoidal
    [1] = irregular parallelogram
    [2] = more or less oval or kidney-shaped
    [3] = subsemicircular
    [4] = fan-shaped

21. Nasal: (Na)
    [0] = tubular but not strongly curved
    [1] = tubular and strongly curved
    [2] = gutter-like or irregularly subrectangular

22. Upper hypurals and second ural: (U2-h)
    [0] = not fused
    [1] = fused

23. Branches of preoperculo-mandibular canal on horizontal arm of preopercle: (Pomc)
    [0] = distributed as separate openings
    [1] = connected with each other to form a horizontal groove

24. Neural spine on u1: (Nu1)
    [0] = absent or rudimentary
    [1] = one complete
    [2] = double (2)

25. The second infraorbital: (Io2)
    [0] = more or less slender and small in size
    [1] = more or less rectangular and moderate in size
    [2] = irregularly wide trapezoidal in shape and large in size

26. Shape of dorsal fin (when it is present): (Dsh)
    [0] = triangular or falcate
    [1] = rounded

27. Posterior rays of dorsal and anal fins: (Prda)
    [0] = shorter than anterior ones
    [1] = longer than or as long as anterior ones

28. Pterygo-quadrate area behind and below orbit: (P-qa)
    [0] = not completely covered by infraorbitals
    [1] = completely covered by infraorbitals

29. Palatine and ectopterygoid: (Paec)
    [0] = separate from each other
    [1] = fused to form palato-ectopterygoid

30. Dorsal arm of post-temporal: (Dapt)
    [0] = less than 1.5 times as long as ventral arm
    [1] = more than twice as long as ventral arm

31. Head of hyomandibular articulating with cranium: (Hmh)
    [0] = single-headed
    [1] = separate double-headed
    [2] = bridged double-headed

32. Shape of dermosphenotic: (Sdsp)
    [0] = irregular triangular
    [1] = triradiate

33. "Cheek wall" formed by enlargement of 1st to 3rd infraorbitals: (CKW)
    [0] = absent
    [1] = present

34. Scales: (Sca)

[0] = not reticulate
[1] = reticulate

35. Length of vertical arm of preopercle (if it is angular in shape): (Lvap)
[0] = longer than horizontal arm
[1] = about as long as horizontal arm

36. Anterior end of horizontal arm of preopercle: (Hap)
[0] = extending anteriorly to beneath orbit or to level of posterior edge of orbit
[1] = extending anteriorly behind orbit

37. Basihyal tooth plate (when it is present) and basibranchial tooth plate: (Bhbb)
[0] = separate from each other
[1] = fused with each other

38. Posterior edge of nasal (when it is gutter-like or irregularly subrectangular): (Pena)
[0] = straight or slightly curved
[1] = strongly curved and extending backward

39. First pectoral fin ray: (Pfr1)
[0] = normal (not enlarged)
[1] = strong (greatly enlarged) and extremely long

40. Angle of jaws: (Ja)
[0] = anterior to middle vertical line of orbit
[1] = between middle vertical line and posterior edge of orbit
[2] = behind orbit

41. Frontal: (Fr)
[0] = posteriorly broader or only slightly narrower than anteriorly
[1] = anteriorly about 1.5 times as broad as posteriorly
[2] = anteriorly greatly expanded to form an anterior portion at least twice as broad as posterior portion

42. Ratio of depth to width of opercle: (Rdwo)
[0] = <2
[1] = >2

43. Shape of extrascapular (supratemporal) when it is present: (Ses)
[0] = expanded and more or less squred or irregular triangular
[1] = slender and distinctly angular or branched

44. Preopercle: (Pop)
[0] = angular with a distinct horizontal arm
[1] = curved with no distinct horizontal arm

45. Hyomandibular: (Hm)
[0] = anterior not extended
[1] = with a greatly extended subtriangular anterior wing

46. Shape of infraorbital 3 (lower infraorbital behind orbit): (Sio3)
[0] = deep and posteriorly deep-fanwised

[1] = irregular rectangular
[2] = elongate and posteriorly shallow-fanwised

47. Infraorbital ledge formed by the lateral extension of the orbital margin of io1 and io2: (IOL)
[0] = absent
[1] = present

48. Infraorbital canal on infraorbitals 1-3: (Ioc)
[0] = enclosed in a bony tuber
[1] = opening in a groove

49. Utriculus: (Utr)
[0] = connected with sacculus and lagena
[1] = completely separated from sacculus and lagena

50. Mouth cleft: (Mc)
[0] = anteriorly directed or slightly upturned
[1] = strongly upturned

51. Shape of anal fin in male and female: (Ash)
[0] = same shape in both sexes
[1] = sexually dimorphic

52. Premaxilla: (Pmx)
[0] = anterior portion raised
[1] = anterior portion not raised
[2] = anterior portion lower than posterior portion

53. Postero-dorsal projection of opercle: (Pdpo)
[0] = absent
[1] = present

54. Mid-dorsal concavity on premaxilla: (Mcpm)
[0] = absent
[1] = present

55. Neural spine on pu1: (Npu1)
[0] = always completely developed
[1] = rudimentary
[2] = absent

56. Number of neural spines on pu2: (#Pu2)
[0] = single
[1] = double or potential to be double

57. Posterior end of maxilla: (Pemx)
[0] = lying on angular
[1] = lying on dentary

58. Antorbital and first infraorbital: (Aio1)
[0] = separate from each other

[1] = fused with each other

59. Tooth plate of basihyal: (Bhtp)
[0] = present
[1] = absent

60. Postero-ventral margin of opercle: (Pmop)
[0] = rounded
[1] = distinctly concave

61. Orbitosphenoid: (Osh)
[0] = present
[1] = absent

62. Supratemporal commissural sensory canal passing through parietals: (Scsc)
[0] = absent
[1] = present

63. Mandibular (dentary) canal: (Mdc)
[0] = enclosed in bony tube
[1] = opening in a groove parallel with ventral edge of dentary

64. Subopercle: (Sop)
[0] = present
[1] = absent

65. Abdominal scutes: (Abs)
[0] = absent
[1] = present

APPENDIX 5-II: Measurements of selected new (complete) specimens of †*Eohiodon woodruffi.*

	TL	SL	BD	HL	HD	PPL	PVL	PDL	PAL	CPL	CPD	FL
FMNH PF9878	99	80	27	19	18	20	32	45	50	16	10	89
FMNH PF9880	80	65	22	18	12	19	29	38	44	13	9	73
FMNH PF9882	173	142	55	30	27	29	60	78	92	25	19	155
FMNH PF10424	177	138	50	30	30	28	62	80	98	24	18	156
FMNH PF10634	70	58	21	19	16	19	26	34	37	14	9	64
FMNH PF10639	122	98	35	24	25	26	46	55	61	19	14	112
FMNH PF10955	38	30	9	8	8	9	16	18	22	5	3	35
FMNH PF12516	200	161	65	35	36	33	69	93	103	29	22	178
FMNH PF13064	110	86	38	22	23	22	41	49	58	17	11	95
ROM 43220	155	125	43	27	27	26	54	77	84	27	17	139
UALVP M3	91	71	23	19	18	19	29	36	42	22	11	81
UALVP 22905	?	126	47	33	32	32	55	74	77	30	17	?
UALVP 31948	217	182	65	43	39	37	83	100	114	33	25	206

Chapter 6

AN EOCENE SPECIES OF *HIODON* FROM MONTANA, ITS PHYLOGENY, AND EVOLUTION OF THE POSTCRANIAL SKELETON IN HIODONTIDAE*

INTRODUCTION

Hiodon is a Recent genus of fishes endemic to the fresh waters of North America. It is represented by two species: *Hiodon tergisus* Lesueur, 1818, the mooneye, and *H. alosoides* (Rafinesque), 1819, the goldeye. *Hiodon tergisus* is easily distinguished from *H. alosoides* in that its dorsal fin origin is anterior to its anal fin, its abdomen has a fleshy keel only between the anal and pelvic fins, and its maxilla extends only to beneath the middle of its eye (Jordan and Evermann, 1896; Glenn, 1975).

Although *Hiodon* has been listed from the Miocene of North America (Smith, 1981), most North American fossil hiodontids have been referred to the genus †*Eohiodon* (Cavender, 1966, 1986; Wilson, 1977, 1978; Grande, 1979, 1984; Wilson and Williams, 1993). Other possible records of the genus †*Eohiodon* from Asia (Sytchevskaya, 1986; Shen, 1989) are here considered doubtful pending additional detailed study. In the North American species, there is a distinct gap between †*Eohiodon* and *Hiodon*, particularly with regard to the opercular system, the upper jaw, and the postcranial skeleton.

Material recently collected from the Eocene-Oligocene Kishenehn Formation of Montana shows features that bridge the morphological gap between †*Eohiodon* and *Hiodon*, and suggests that the *Hiodon* lineage had evolved as early as the late Eocene.

The goals of this chapter are to describe a new species of *Hiodon* based on two specimens from the Kishenehn Formation of northwestern Montana, and to discuss the evolution of the postcranial skeleton in the Hiodontidae based on a preliminary

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*A version of this chapter has been published: Li Guo-qing and M. V. H. Wilson. 1994. An Eocene species of *Hiodon* from Montana, its phylogenetic relationships, and the evolution of the postcranial skeleton in the Hiodontidae (Teleostei). Journal of Vertebrate Paleontology, 14(2): 153-167; USA.

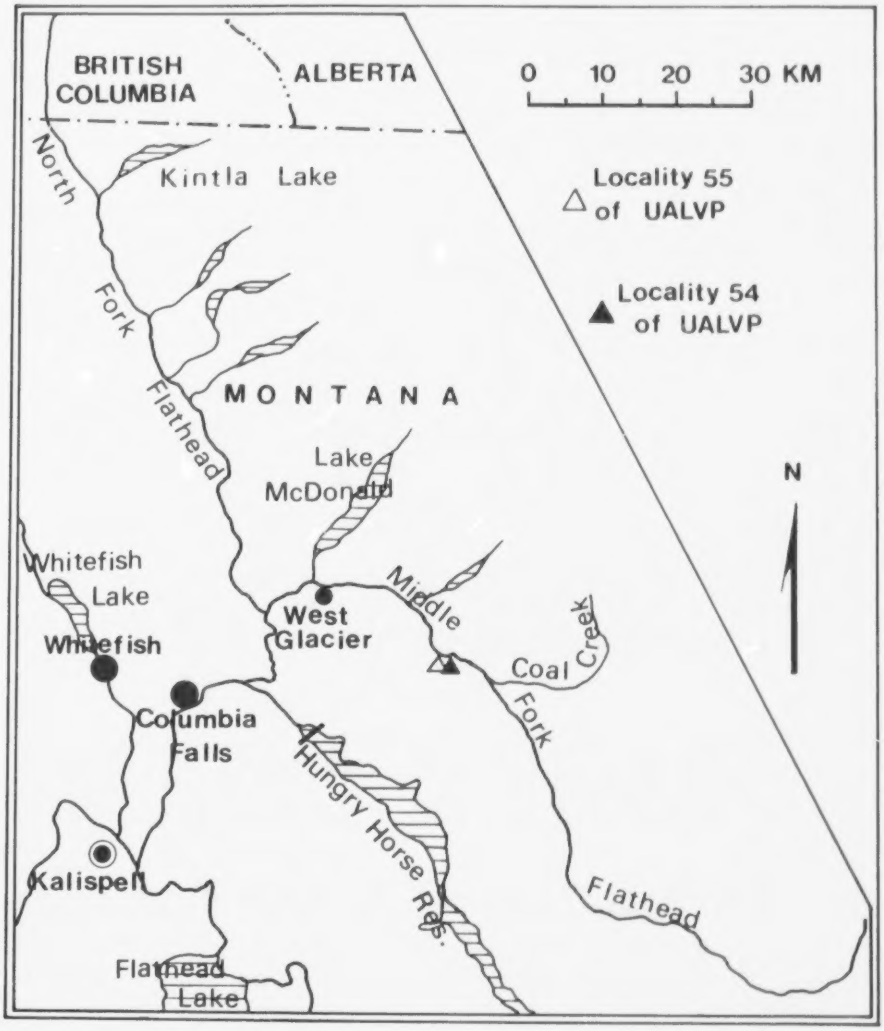

BRITISH COLUMBIA
ALBERTA
0 10 20 30 KM
Locality 55 of UALVP
Locality 54 of UALVP
North Fork Flathead
Kintla Lake
MONTANA
Lake McDonald
N
Whitefish Lake
Whitefish
West Glacier
Middle Fork
Coal Creek
Columbia Falls
Hungry Horse Res.
Kalispell
Flathead
Flathead Lake

FIGURE 6-1: Map showing the fossil localities and the main part of the Flathead River system, along which the Kishenehn Formation is exposed.

phylogenetic analysis of fossil and Recent Hiodontidae.

Geology

The Kishenehn Formation represents freshwater deposits that accumulated "during the Eocene (?), Oligocene, and Miocene (?)" (Constenius et al., 1989) in the Kishenehn Basin of northwestern Montana and southeastern British Columbia. Strata in this formation exposed along cut banks of the Flathead River system consist of interbedded conglomerates, sandstones, siltstones, mudstones, marlstones, coals, and oil shales (Constenius et al., 1989). These deposits are grouped in three members, the Basal Member, the Coal Creek Member and the Pinchot Member. The fossil fish specimens described in this chapter were collected from oil shales of the Coal Creek Member exposed along the Middle Fork of the Flathead River (Fig. 6-1). The fish-bearing strata of the Coal Creek Member are thought to be late Eocene in age (K. Constenius, pers. comm.). The new hiodontid species is comparatively rare while a species of the catostomid genus †*Amyzon* is abundant (Constenius et al., 1989). The Kishenehn Formation has also yielded fossils of plants, insects, mollusks, and mammals at various localities (Russell, 1952, 1954, 1956; Hopkins and Sweet, 1976; McMechan, 1981; Constenius et al., 1989).

Comparative Materials

Specimens studied for this chapter consist of Recent dried skeletons, fossil, and preserved Recent specimens.

Lycopteriformes– Specimens listed in Chapter 5.

Hiodontiformes– Hiodontidae: *Hiodon alosoides* (Rafinesque), one cleared-and-stained specimen (UAMZ 3969), 22 adult (UAMZ 3155, 3158a-e, 3160a-e, 3161a-e, 3200, 3455, 3543a-b, and two uncataloged specimens from the North Saskatchewan River near Edmonton, Alberta, SL ranging from 258 to 317) (Appendix 6-II); and 20 juvenile (UAMZ 4044, research collection from Mamawi/Claire lakes, Alberta, SL ranging from 63 to 83) preserved specimens (Appendix 6-III). *Hiodon tergisus* Lesueur, 39 adult specimens, of which 12 were collected from the Red Deer River (UAMZ 4389, 4588-4596, and 4602-4603, SL ranging from 196 to 267) (Appendix 6-IV); 27 from the North Saskatchewan River, Edmonton (UAMZ 4568-4587, 4597-4601, 4612, and 4651, SL ranging from 215 to 263) (Appendix 6-V). †*Eohiodon rosei* (Hussakof), UALVP 12436 and specimens listed in Cavender (1966). †*Eohiodon woodruffi* Wilson, specimens examined in Chapter 5. †*Yanbiania wangqingica* Li, specimens listed in Li

(1987). †*Plesiolycoptera daqingensis* Chang and Chou, specimens listed in Zhang and Zhou (1976).

Osteoglossiformes– Osteoglossidae: *Osteoglossum bicirrosum* and *O. ferreirai*, specimens listed in Chapter 2. †*Phareodus testis* and †*Phareodus encaustus*, specimens studied in Chapter 2. †*Phareodus queenslandicus*, specimens listed in Chapter 2. *Arapaima gigas*, specimens listed in Chapter 2.

Pantodontidae: *Pantodon buchholsi*, specimens listed in Chapter 2

Notopteridae: *Chitala chitali* and *Xenomystus nigri*, specimens listed in Chapter 2.

SYSTEMATIC PALEONTOLOGY

Subdivision TELEOSTEI Müller, 1846
Superorder Osteoglossomorpha Greenwood et al., 1966
Order Hiodontiformes *sensu stricto*
Family Hiodontidae Valenciennes 1846

Included Genera– *Hiodon*, †*Eohiodon*, †*Plesiolycoptera*, †*Yanbiania*.

Emended Diagnosis– Dermosphenotic triradiate, opercle an irregular parallelogram, articulation facet for quadrate constructed by articular and angulo-retroarticular, dorsal part of hyomandibular distinctly separate or bridged and double-headed, dorsal arm of post-temporal more than twice as long as ventral arm, pelvic fin seven-rayed, anal pterygiophores at least equal in number to dorsal pterygiophores.

Remarks– In order to clarify the membership of the Hiodontidae, I have also tried to assess which taxa belong in the †Lycopteridae from among the species included by Takai (1943), Liu et al. (1963), and Yakovlev (1965). These authors included "a number of rather ill-defined genera" (Greenwood, 1970). I have conservatively recognized only two valid genera in this family (see Table 6-3). Regarding †*Lycoptera*, only the best known species †*L. middendorffii* (Müller, 1847) and †*L. davidi* (Sauvage) (Woodward, 1901; Gaudant, 1968; Ma, 1987) are considered to be valid in this thesis.

It is true that the articulation facet for the quadrate in †*Lycoptera* and †*Tongxinichthys* (Ma, 1980) may be also constructed by all three elements. However, the angular is not fused with the retroarticular but with the articular [the "angular" labelled in Greenwood (1970), and Ma (1980) is the retroarticular].

Gaudant (1968) and Ma (1987) counted 7-8 pelvic fin rays in †*Lycoptera davidi*.

Greenwood (1970) listed 7-9 pelvic rays in various species, but did not mention which species were counted. However, my examination of all the IVPP specimens that have pelvic fins and were referred to †*L. davidi* by Liu et al. (1963), including the specimens examined by Ma, found only four to five, rarely six, and never more than six rays. Perhaps counts by earlier authors included rays from both pelvic fins.

Genus *Hiodon* Lesueur, 1818

Type Species– *Hiodon tergisus* Lesueur.

Included Species– *H. tergisus*, *H. alosoides*, †*H. consteniorum* sp. nov.

Emended Diagnosis– This genus differs from all other genera in the family in having: nasal tubular and curved, premaxilla with mid-dorsal concavity and no anterior process, preopercle with a postero-ventral rounded expansion, opercle with an acute postero-dorsal projection and a protruding upper posterior border, 50-63 vertebrae, neural spine on first preural centrum reduced or absent, two neural spines usually developed on the second preural.

Remarks– *Hiodon tergisus* differs osteologically from *H. alosoides* in having fewer vertebral centra (55-58 versus 59-61 or 63), fewer anal pterygiophores (27-30 versus 31-36), fewer principal anal fin rays (28-30 versus 31-33), more dorsal pterygiophores (13-15 versus 10-12), and more principal dorsal fin rays (11-13 versus 9-10) (Cavender, 1966; Grande, 1979; pers. obs.). These two Recent species are also distinguishable by several proportions: e.g., *H. alosoides* has a relatively longer predorsal length, a longer anal fin base, a relatively lower body depth, and a shorter dorsal fin base for its size than *H. tergisus*.

†*Hiodon consteniorum* sp. nov.

(Figs. 6-2 to 6-5)

Holotype– UALVP 38875, a well-preserved presumed male (Fig. 6-2A), SL=61, collected by John and Leona Constenius of Whitefish, Montana.

Allotype– UALVP 24200, an almost complete presumed female (Fig. 6-2B), SL=65, collected by M. V. H. Wilson and L. A. Lindoe.

Locality– The holotype is from UALVP Locality No. 55, and the allotype from UALVP Locality No. 54, in river cuts of the Middle Fork of the Flathead River, Montana (Fig. 6-1).

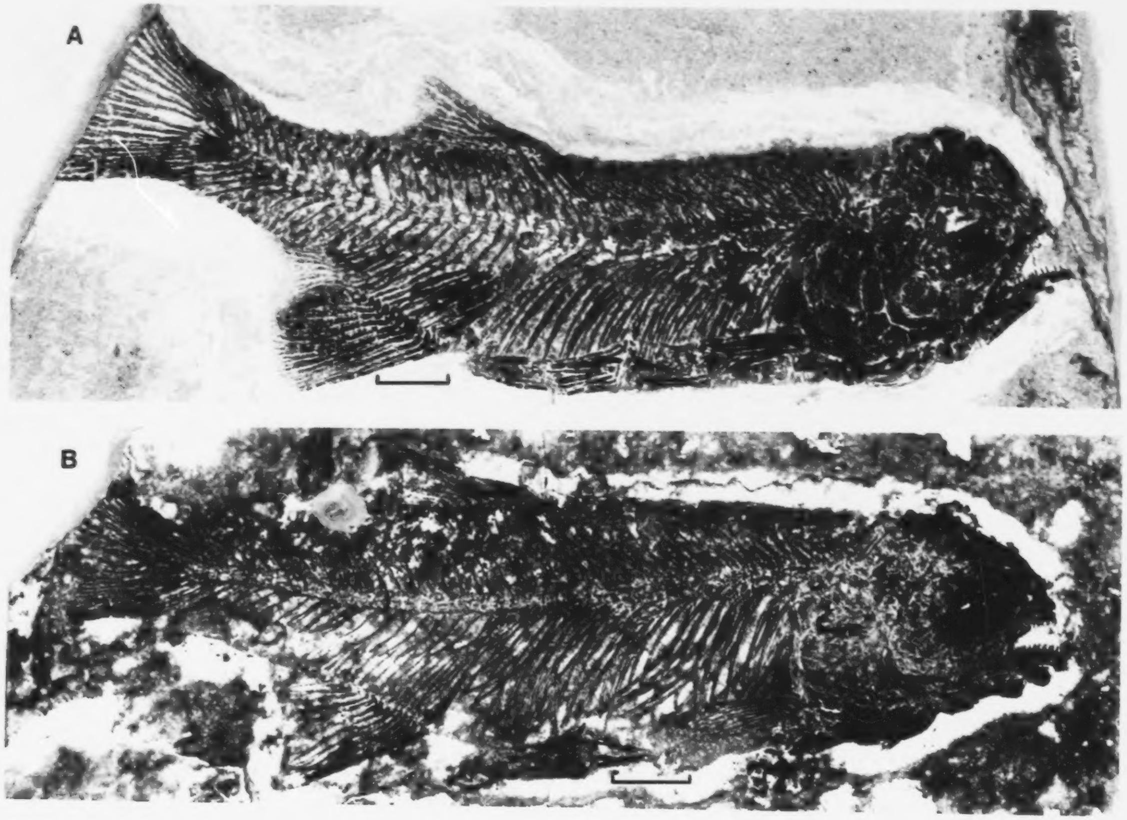


FIGURE 6-2: Photo of †*Hiodon consteniorum* sp. nov. **A**, holotype, UALVP 38875, SL=61. **B**, allotype, UALVP 24200, SL=65. Scale bars equal 5mm.

Horizon– Coal Creek Member of the Kishenehn Formation (Constenius et al., 1989), late Eocene in age.

Diagnosis– A species of *Hiodon* differing from the two Recent species as follows: mid-dorsal concavity on premaxilla deeper and narrower, posteriorly more expanded maxilla extending not beyond posterior 1/3 of orbit, basihyal tooth plate longer (more than 3/5 versus about 1/2 as long as lower jaw in Recent species), fewer vertebrae (52-53 versus 55-61 or 63 in Recent species), and fewer anal pterygiophores (20 versus 27-36 in Recent species).

Remarks– This new species can also be distinguished from the two Recent species by the following ratios: SL to BD ratio about 3.3-3.6 (versus 3.0-3.1 in *H. tergisus* and 3.3-3.4 in *H. alosoides*), PDL to PAL ratio about 0.83-0.84 (versus 0.92-0.93 in *H. tergisus* and 1.06-1.11 in *H. alosoides*), and AFBL to DFBL about 1.24-1.35 (versus 2.02-2.04 in *H. tergisus* and 2.74-3.12 in *H. alosoides*).

Etymology– The specific name honors the Constenius family (Dr. J. N. Constenius, Leona Constenius, and Kurt Constenius) for their discovery of the fossil locality, for donating the holotype for this study, and for their many other contributions to paleontology.

Description

Only two specimens, designated here as the holotype and allotype, are available. They are exposed from the right side and both have an incomplete caudal fin.

Measurements of Type Specimens– The holotype has SL=61, BD=17, HL=18, HD (uppermost part of parietal to ventral border of the horizontal arm of preopercle)=14, PPL=19, PVL=30, PDL=35, PAL=42, CPL=12, CPD (close to the base of the caudal fin, as in the Recent *Hiodon* species)=8, DFBL=9, AFBL=12.

The allotype has FL=65, SL=60, BD=18, HL=18, HD=14, PPL=17, PVL=30, PDL=35, PAL = 41, CPL=11, CPD=7, DFBL=8, AFBL=10.

Neurocranium and Skull Roof– As in the Recent *Hiodon*, the nasal (Fig. 6-3) is slender and tubular in shape. It is bent at an approximately 140° angle at a point anterior to the center of the bone on both the holotype and allotype. The two nasals are separated by the mesethmoid; the latter resembles that of the Recent *Hiodon* in shape.

The frontal is similar in outline to that of the Recent *Hiodon*, being broader posteriorly than anteriorly and having a zigzag anterior edge. As in the Recent species the suture between the two frontals is straight. The supraorbital sensory canal on the frontal is enclosed in a curved bony tube that extends anteriorly to the nasal.

The parietal (Fig. 6-3) appears similar to that in the Recent *Hiodon*. This bone is posteriorly covered by the crushed supratemporal on the allotype. The concave postero-medial margin shown on the right parietal of the holotype suggests that the two parietals are posteriorly separated by the supraoccipital, which is difficult to identify in both specimens. The suture between the parietal and the frontal is nearly straight.

The otic-temporal region is rather well preserved on the holotype. The temporal fenestra is present at the same position as in the Recent *Hiodon*. It is bordered dorsally by the narrower posterior part of the parietal, ventrally by the dermopterotic, and posteriorly by the epiotic (Fig. 6-3). The dermopterotic is subtriangular and similar to that of Recent *Hiodon* in shape. The epiotic is partially covered by the broken posttemporal and is irregular in shape.

The parasphenoid is typically hiodontid, with the ascending arm and the occipital arm postero-dorsally upturned. The teeth on the ventral side of this bone are relatively larger and stronger than those in *Hiodon*, but similar to those in the Eocene †*Eohiodon* both in shape and size.

Opercular Series– The opercular series is completely visible on the holotype (Figs. 6-2A and 6-3) although this region is partly crushed. There is no scale covering in this region.

The preopercle is similar to that in Recent *Hiodon* in shape, having an upper, vertical arm slightly longer and narrower than the lower, horizontal arm, and a postero-ventral rounded expansion. The two arms of this bone form an approximately 90° angle. As in Recent *Hiodon*, the preopercular sensory canal extends within a bony tube along the anterior margin of this bone, giving off five branches.

The opercle is shaped like that in Recent *Hiodon* species, having an acute postero-dorsal projection and a protruding upper posterior border. Sculpturing is absent. The subopercle is almost identical to that of the Recent *Hiodon*, which has a slightly concave dorsal border to fit the convex ventral border of the opercle, and a rounded ventral border. The interopercle is preserved, but not sufficiently to interpret its shape.

Circumorbital Region– This region is badly crushed and greatly deformed on the allotype but better preserved on the holotype. Structurally this region is similar to that in Recent *Hiodon*. The orbit is bounded dorso-medially by the orbitosphenoid, pterosphenoid, and basisphenoid, with the latter ventral to the pterosphenoid, although all three bones are badly deformed. A dermal supraorbital is apparently absent. Postero-dorsal to the orbit is the prootic, which is partly covered by a displaced dermosphenotic that closely resembles the same element in the Recent *Hiodon*.

As evidenced by the holotype, the infraorbital series (Fig. 6-3) is almost identical to that in Recent *Hiodon* (Nelson, 1969; Greenwood, 1970; pers. obs.) in both the number of elements comprising this series and the shape of most of the elements. The only difference is that the 2nd infraorbital is larger than that in the two Recent species. The infraorbital sensory canal passes through each of the infraorbitals within a tube.

A complete right antorbital is preserved on the holotype with its interior surface exposed. As in the Recent *Hiodon*, this dermal bone also has an orbito-marginal crest.

Jaws– The upper and lower jaws are similar to those of Recent *Hiodon* both in structure and shape, with the mouth cleft not extending posteriorly to the vertical mid-line of the orbit.

The premaxilla is well preserved and exposed on the holotype (Fig. 2). It is elongate with a mid-dorsal concavity. As in Recent *Hiodon*, the anterior portion of this bone is not raised; it is perforated by two openings, of which the anterior one is larger than the posterior one. Teeth on this bone are strong and sharply conical in shape, arranged in a single row.

The maxilla is relatively stouter than that in Recent *Hiodon*. It is more expanded posteriorly and extends approximately to beneath the posterior 1/2-1/3 of the orbit (as in *H. tergisus*). The teeth are arranged in one row and are slightly smaller than those on the premaxilla. A supramaxilla is apparently absent in this species.

The dentary is slender and more similar in shape to that of the Recent *Hiodon* than it is to that of †*Eohiodon*. Its conical teeth resemble those on the premaxilla in size (as also in the Recent *Hiodon*) and are present in at least three rows on the allotype. The mandibular sensory canal passing through this bone is embedded in a bony tube that extends along the ventro-lateral side, opening via five to six pores.

The angular and retroarticular appear to have been fused with each other to form a compound bone, the angulo-retroarticular. This compound bone inserts in the posterior notch of the dentary and carries an articulation facet for the quadrate. The articular lies medial to the angulo-retroarticular. As in Recent *Hiodon*, a postarticular process of the angular (Nelson, 1973) is developed and forms the posterior part of the articulation facet for the quadrate.

Palatopterygoid Arch– This region is somewhat deformed and covered by the infraorbitals and upper jaw on both the holotype and the allotype.

The toothed palatine is ventrally exposed on the holotype; it seems to be identical to that in Recent *Hiodon* in both its shape and number of tooth rows (two to three).

The ectopterygoid is visible on both the holotype and the allotype. As in the Recent

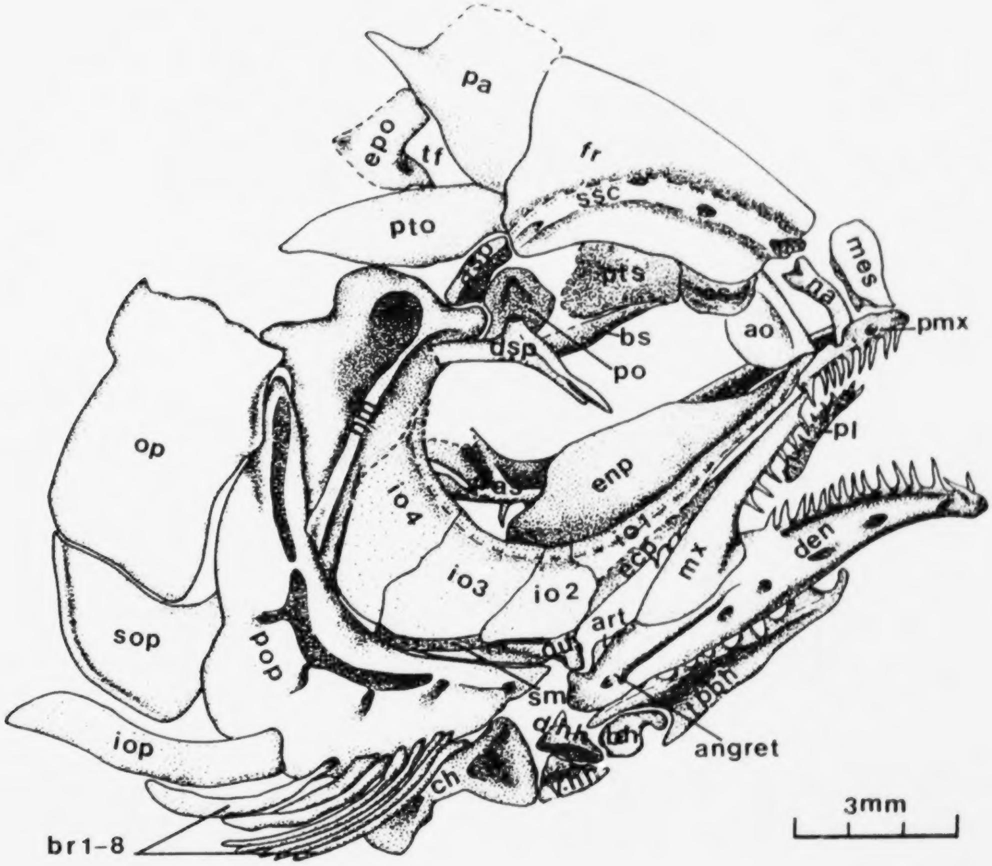

pa
epo
tf
fr
ssc
pto
pts
mes
na
pmx
ao
bs
dsp
po
op
pl
enp
as
io4
io3
io2
ecp
mx
den
art
qu
sop
pop
sm
dhh
bh
vhh
angret
iop
ch
br1-8
3mm

FIGURE 6-3: Diagram showing the skull of the holotype of †*Hiodon consteniorum* sp. nov.

Hiodon species, it is rather slender and slightly curved, and is also a toothed bone.

The endopterygoid can be seen on the holotype. It is very thin and much broader than the ectopterygoid, having its dorsal edge slightly beyond the dorsal crest of the parasphenoid and its narrow anterior end extending anteriorly to beneath the antorbital. Small teeth are distributed mainly on the medio-ventral portion of this bone, as are the teeth on the endopterygoid of the Recent *Hiodon*.

The metapterygoid is wholly covered by io3 and io4-5. It is somewhat U-shaped and similar to that in Recent *Hiodon*.

The quadrate has a relatively larger articulation head; it and the symplectic are more similar to the corresponding bone in the Recent *Hiodon* than to that in †*Eohiodon*.

Hyoid Arch– All elements but the epihyal of this arch can be seen on the holotype (Fig. 6-2A and 6-3).

The hyomandibular has the same pattern as that in Recent *Hiodon*. It bears a well-developed opercular process that is covered by the opercle and articulates with the cranium by two bridged heads; the anterior head contacts the prootic and the autosphenotic, and the posterior the autopterotic. Also as in Recent *Hiodon*, a very strong vertical lateral crest extends from the anterior head to the ventral end of the bone.

The ceratohyal has the shape of an hourglass. Anterior to the ceratohyal are two irregularly shaped dorsal and ventral hypohyals; the former is possibly penetrated as in the Recent *Hiodon*.

The hyoid arch ends ventrally in a subtriangular bone identified as the basihyal, according to its position in the posterior notch of the tooth plate.

The tooth plate of the basihyal is exposed completely on the holotype and partly on the allotype, ventral to the dentary. It is almost identical to that in the Recent *Hiodon* in both its shape and tooth pattern. The only difference is that it is longer than that in the two Recent species (more than 3/5 versus about 1/2 of the length of the lower jaw in the two Recent species).

At least eight and seven curved branchiostegals are present respectively on the holotype and allotype; the upper (posterior) one or two are relatively broader than the lower (anterior) ones. All of these branchiostegals are similar in shape and arrangement to those of other hiodontids.

Cephalic Lateral Line System– The cephalic lateral line system has the same general pattern as that in the Recent *Hiodon* (Greenwood, 1970; Nelson, 1972). An exception is that, unlike specimens of *Hiodon* studied by Greenwood (1970: p. 271, figs. 2 and 4) and Taverne (1977, p. 22: figs. 2-4), the supraorbital sensory canal does not extend to the parietal in this new species. A similar condition is also present in UAMZ 6714, a specimen of the Recent *Hiodon alosoides*, in which the supraorbital canal does not extend to the parietal. As in the Recent *Hiodon*, the end of the infraorbital sensory canal at the anterior end of the first infraorbital bone is very close to the anterior end of the supraorbital canal in the nasal bone.

Vertebral Column– Although most of the precaudal vertebrae (=abdominal vertebrae; Grande, 1979) are crushed and disarticulated or displaced on both the holotype and the allotype, a complete count of vertebrae can still be made with the help of the neural arches in estimating the anteriormost vertebrae. Altogether 52 to 53 vertebrae can be enumerated from both specimens, with 25 caudals (including two urals) and 27 or 28 precaudals (including the first two or three that are anterior to the cleithrum and bear neural spines but no ribs). The neural arches on the precaudal vertebrae are not fused with the centra; the left and right halves of these arches and their spines are autogenous, as are those in the Eocene †*Eohiodon* and the Recent *Hiodon*. The normal centra are horizontally ridged, with a large perforation for the notochord; their length is approximately equal to their depth. Large parapophyses are present on the precaudals. Nineteen sigmoid supraneurals are seen on the holotype and allotype; they lie between the neural spines of the precaudals, with the first in the space between the second and the third neural spines and the last just in front of the first dorsal pterygiophore.

Small epineurals are present in the region just dorsal to the precaudals. Slender pleural ribs number 46 to 48, and appear to articulate above and behind the parapophyses and extend to the ventral quarter of the wall of the body cavity.

On the caudal vertebrae anterior to the second preural both the neural and the haemal arches are fused with the centra.

Caudal Skeleton– The caudal skeleton consists of two upturned urals and four preural centra supporting the caudal fin rays (Fig. 6-4 and 6-5).

As in †*Eohiodon* and Recent *Hiodon* there are seven hypurals, which decrease in depth and length dorsally. Hypural 1 is the broadest, with a rather expanded distal end; its proximal end narrows distinctly to form a head that articulates but does not fuse with the first ural centrum. Hypural 2 is slightly shorter and less deep than hypural 1, with a rounded proximal end. These two lower hypurals, articulating with the first ural, together support the lower lobe of the caudal fin. Hypurals 3 to 7 are slender; of these five elements only hypural 3 articulates directly with the second ural. These upper hypurals are arranged in the same pattern as those in other hiodontids and support the upper lobe of the caudal fin.

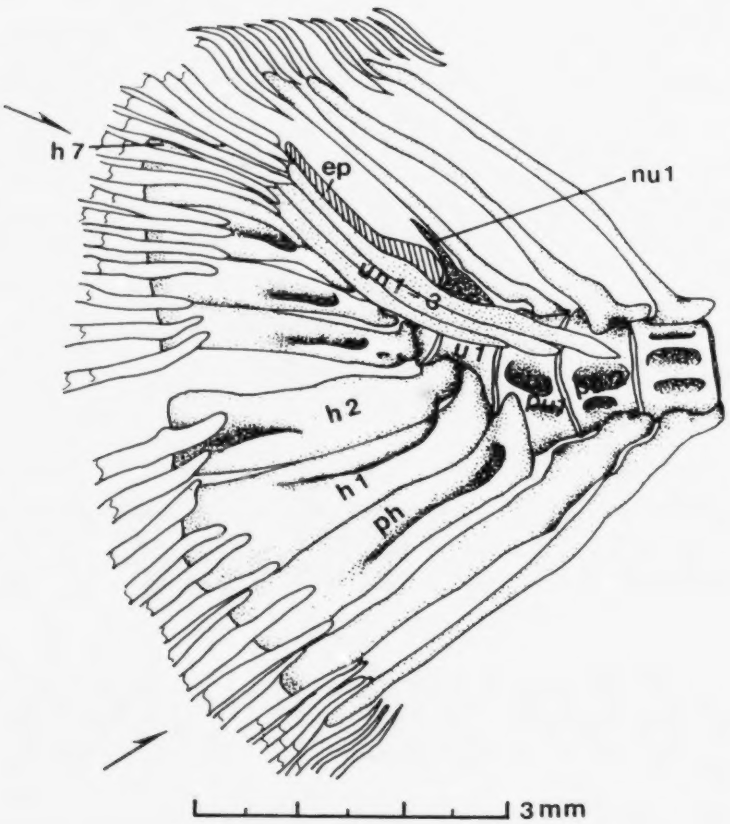

h7
ep
nu1
un1-3
u1
pu2
pu1
h2
h1
ph
3mm

FIGURE 6-4: Caudal skeleton of the holotype of †*Hiodon consteniorum* sp. nov.

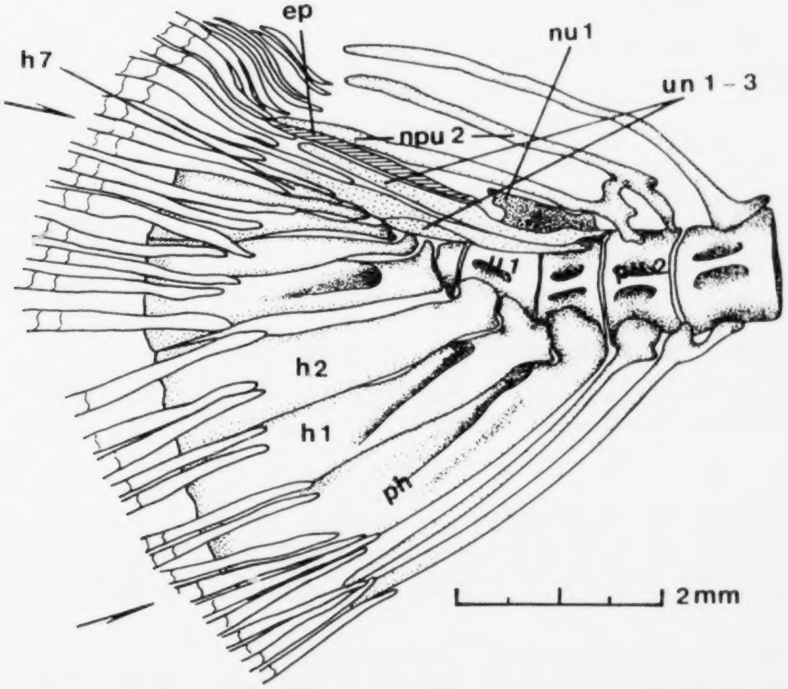

ep
h7
nu 1
un 1 – 3
npu 2
u1
pu2
h2
h1
ph
2 mm

FIGURE 6-5: Caudal skeleton of the allotype of †*Hiodon consteniorum* sp. nov., showing the second preural centrum bearing two neural spines.

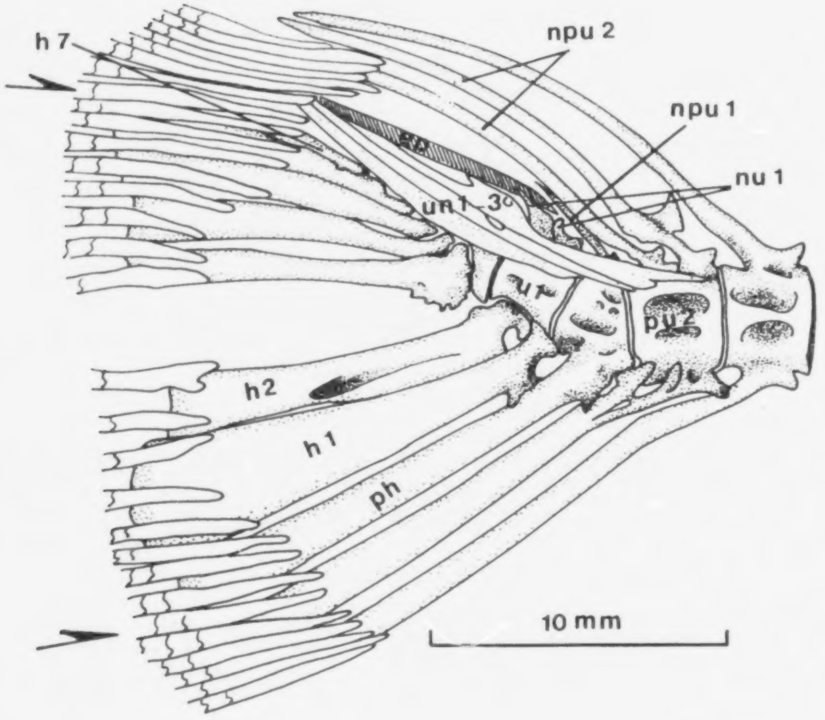

h 7
npu 2
npu 1
nu 1
ep
un1-3°
ut
pu2
h2
h1
ph
10 mm

FIGURE 6-6: Caudal skeleton of the Recent *Hiodon alosoides*, based on UAMZ 6714, collected from the North Saskatchewan River, near Edmonton, Alberta.

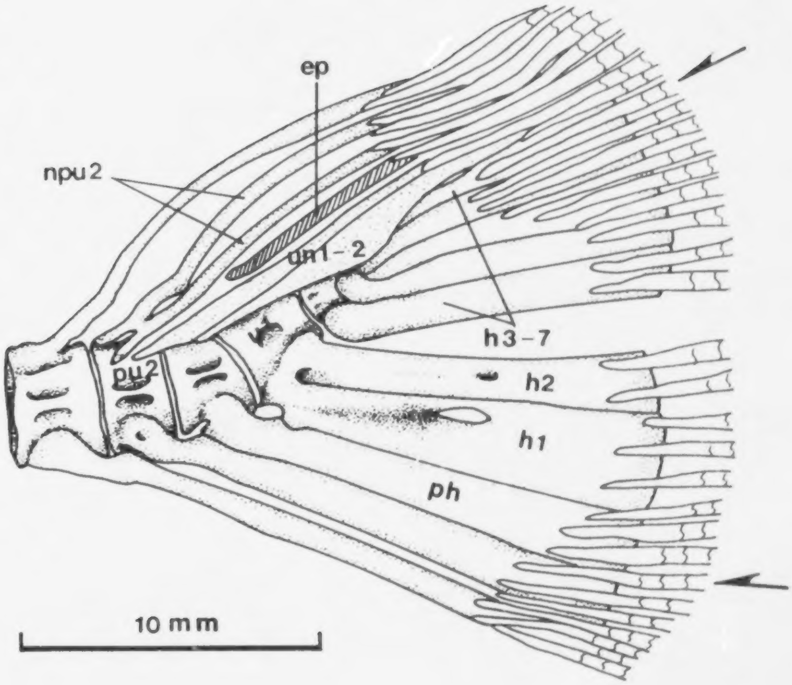

ep
npu2
un1-2
h3-7
pu2
h2
h1
ph
10 mm

FIGURE 6-7: Caudal skeleton of the Recent *Hiodon tergisus*, based on UAMZ 4389, collected from the Red Deer River, near Red Deer, Alberta.

Three uroneurals are present on both specimens; the first (the anteriormost) extends anteriorly to the dorsal margin of the second preural centrum. As in †*Yanbiania*, †*Eohiodon*, and Recent *Hiodon*, there is only one slender epural dorsal to the anteriormost uroneural.

The parhypural is strong, with a distinct ridge extending from near its head, which is articulated but not fused with the first preural, to the distal end of this bone. This is different from Recent *Hiodon*, in which the parhypural is fused with the preural 1 and not typically ridged (Fig. Figs. 6-6 and 6-7).

As in UAMZ 6714 (Fig. 6-6) of *Hiodon alosoides* and UAMZ 4389 (Fig. 6-7) of *H. tergisus*, the second preural centrum of the allotype bears two complete neural spines that extend postero-dorsally to support the anterior upper procurrent rays of the caudal fin (Fig. 6-5). The neural spine on the first preural is not developed, perhaps replaced by the single epural.

Girdles and Paired Fins– The pectoral girdle is not well preserved. The supracleithrum is badly crushed on the allotype but can be seen on the holotype. As in Recent *Hiodon*, it is knife-shaped, with a relatively straight anterior edge and a curved posterior edge. It is not certain whether there is a postcleithrum (it may be covered by the upper part of the cleithrum). The cleithrum is falcate and similar to that in the other hiodontids both in shape and proportion.

The posttemporal is exposed on the allotype. It is forked, with a slender dorsal arm approximately two times as long as the ventral arm.

The ventrally located pectoral fin consists of 12 fin rays; the first is the longest and distally segmented but unbranched. The others are both segmented and branched.

The pelvic girdle consists of two tapering innominata [Men et al., 1987, synonym of pelvic fin support (Grande, 1979) and pelvic bones (Wilson, 1978)], which are approximately half as long as the longest pelvic fin ray. Seven pelvic fin rays are present. The distance between the origins of the pelvic fin and the pectoral fin is greater than that between the origins of the pelvic fin and the anal fin.

Dorsal and Anal Fins– The dorsal fin is falcate and triangular in lateral view, with a moderately concave posterior margin. It originates anterior to the anal fin by six vertebral centra on the holotype and by eight centra on the allotype, and ends above the anterior fifth of the anal fin on both specimens. In total 16 fin rays are present, of which the last 13 are principal rays and the first three accessory. Of the 13 principal dorsal rays, the first is distally segmented but not branched; others are both segmented and branched, and the last is divided to the base. Fourteen distally expanded dorsal pterygiophores (proximal radials) are present on both specimens to support the dorsal fin. These dorsal pterygiophores decrease in length posteriorly.

The anal fin is larger than the dorsal fin, with its base approximately 1.3 to 1.4 times as long as that of the dorsal fin. Its border on the male holotype is posteriorly concave but anteriorly convex, indicating that the anal fin in this new species also is sexually dimorphic (Fig. 1). Five accessory and 18 principal rays are present on both specimens. Of the 18 principal anal fin rays, the first is unbranched, the others are both segmented and branched, and the last one is divided to the base (double). At least 20 anal pterygiophores are present; the anteriormost three support the five accessory rays and the first unbranched principal ray, while the others have a one-to-one relationship with the branched fin rays.

Caudal Fin– The distal part of the caudal fin has been deformed or is incomplete on both the holotype and the allotype. However, the proximal part is complete and well preserved. This fin is definitely forked and consists of eight branched and one unbranched principal rays in each of its lower and upper lobes. The lower procurrent rays number 16 on the holotype and 11 on the allotype, and the upper procurrent rays 19 on the holotype and 14 on the allotype. The fin rays (including the procurrent rays) in the lower lobe are supported by the two lower hypurals, the parhypural on the first preural centrum, and the slender and elongate haemal spines on the second, third, and fourth preurals. The fin rays in the upper lobe are supported by five upper hypurals, three uroneurals, the single epural, and the neural spines on the preural centra 2 through 4 on the holotype, or the two neural spines on the second preural on the allotype.

Scales– Judging from the remnants of the scales on both specimens, the scales are cycloid, being similar to those in †*Eohiodon* and the Recent *Hiodon*, which are higher than broad, with mainly basal radii.

DISCUSSION

i: Phylogenetic Relationships

Although †*Hiodon consteniorum* sp. nov. is comparable to †*Yanbiania* in possessing 14 dorsal pterygiophores (see Li, 1987: table 1), it has a stronger resemblance to Recent species of *Hiodon* in some of the other meristic characters listed in Tables 6-1 to 6-3, in the shape of the nasals, frontals, and parietals, and in the shape and structures of the lower and upper jaws, the palatopterygoid and hyoid arches, the opercular system, and

TABLE 6-1: Meristics of *Hiodon alosoides* listed in Appendices 6-II and 6-III.

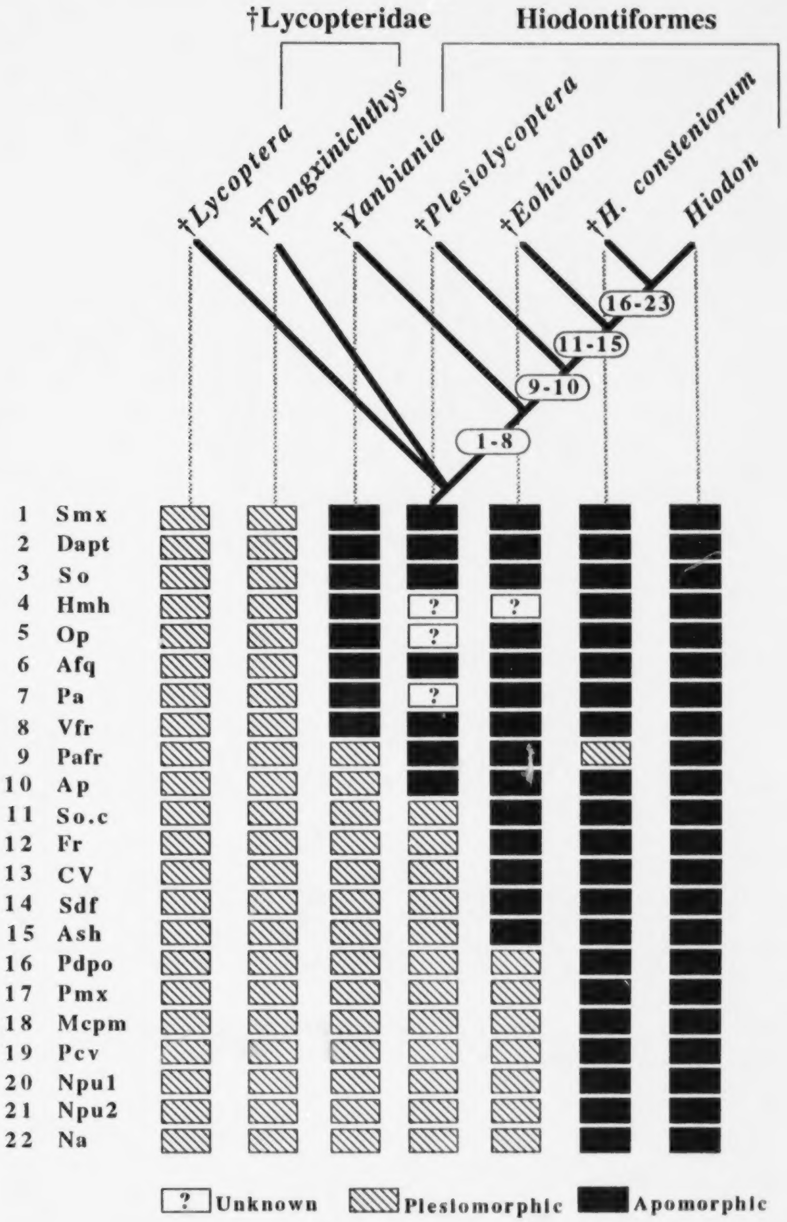
UAMZ SPECIMENS	BR	PFR	VFR	DFR	AER	CFR
3161-a	9	13	7	10	32	16
3161-b	9	12	7	9	32	16
3161-c	9	12	7	11	32	16
3161-d	8	12	7	10	33	16
3161-e	9	12	7	10	32	16
3155	10	12	7	10	33	16
3200	10	12	7	10	33	16
3158-a	8	11	7	10	33	16
3158-b	8	12	7	9	33	16
3158-c	9	11	7	11	32	16
3158-d	9	12	7	10	33	16
3158-e	10	11	7	10	32	16
3160-a	9	11	7	10	32	16
3160-b	8	11	7	9	31	16
3160-c	8	12	7	9	33	15
3160-d	10	12	7	10	31	16
3160-e	10	11	7	11	32	16
3455	9	12	7	10	32	16
3543-a	9	12	7	10	31	16
3543-b	10	12	7	11	32	16
5	8	13	7	9	32	16
6	10	12	7	9	32	16
7	10	12	7	9	31	16
8	10	12	7	10	32	16
9	10	13	7	10	31	16
10	10	13	7	10	32	16
11	9	12	7	9	33	16
12	8	13	7	9	32	16
13	9	12	7	9	32	16
14	9	13	7	10	32	16
15	9	13	7	9	31	16
16	9	13	7	10	33	16
17	9	12	7	10	31	16
18	9	12	7	10	33	16
19	10	12	7	10	32	16
20	9	12	7	10	32	16
21	9	13	7	10	32	16
22	10	12	7	10	32	16
23	9	13	7	10	32	16
24	10	12	7	10	32	16
AVERAGE	9.18	12.10	7.00	9.83	32.08	15.98

TABLE 6-2: Meristics of *Hiodon tergisus* listed in Appendices 6-IV and 6-V.

UAMZ SPECIMENS	BR	PFR	VFR	DFR	AFR	CFR
4571	8	12	7	11	28	16
4575	9	12	7	13	29	16
4587	9	12	7	11	28	16
4573	9	12	7	12	28	16
4612	9	13	7	12	31	16
4577	9	13	7	12	29	14
4583	8	13	7	12	29	16
4586	9	13	7	12	29	16
4568	8	13	7	12	28	16
4597	8	13	7	12	26	16
4584	8	13	7	13	29	16
4570	8	13	7	13	30	16
4576	8	13	7	11	29	16
4569	9	13	7	13	28	16
4580	9	13	7	11	28	16
4601	9	13	7	12	28	16
4581	9	13	7	12	28	16
4651	8	13	7	12	28	16
4600	8	12	7	13	29	16
4598	8	13	7	11	28	16
4572	8	13	7	12	29	16
4574	8	12	7	12	28	16
4599	8	13	7	11	28	16
4578	8	13	7	12	28	16
4579	9	13	7	12	28	16
4582	9	13	7	12	29	16
4585	8	13	7	12	27	16
4389	10	13	7	13	27	16
4595	9	12	7	13	29	16
4594	10	12	7	13	28	16
4596	9	12	7	12	29	16
4589	9	12	7	13	29	16
4592	9	12	7	13	29	16
4588	9	13	7	13	29	16
4590	8	13	7	12	28	16
4591	9	12	7	12	28	16
4603	9	12	7	12	29	16
4593	10	12	7	13	30	16
4602	9	12	7	13	28	16
AVERAGE	8.67	12.62	7.00	12.18	28.46	15.95

TABLE 6-3: Comparison of some meristic characters among species in Hiodontiformes and †Lycopteriformes. *H.*, *Hiodon;* †*E.*, †*Eohiodon;* †*P.*, †*Plesiolycoptera;* †*Y.*, †*Yanbiania;* †*T.*, †*Tongxinichthys;* †*L.*, †*Lycoptera.*

	BR	VC			PFR	VFR	DFR	DP	AFR	AP
		PCV	CV	Total						
H. alosoides	8-10	33	25-28	58-63	11-13	7	9-11	10-12	31-33	31-36
H. tergisus	8-10	32-33	23-25	55-58	12-13	7	11-13	13-15	26-30	27-31
†*H. consteniorum sp. nov.*	8	27-28	25	52-53	12	7	13	14	18	20
†*E. woodruffi*	8-10	22-24	23-26	45-50	12-13	7	12-15	14-16	17-20	19-20
†*E. falcatus*	8-10	22-24	25-26	47-50	12-13	7	12-14	14-17	22-24	21-24
†*E. rosei*	7- 9	22-24	24-25	44-49	10-13	7	11-13	13-15	14-18	16-19
†*P. daqingensis*	?	20+	21	41-42	11	7	11	11	20	22
†*Y. wangqingica*	7+	22-23	22-23	44-46	12	7	12-13	14	12-13	14
†*T. microdus*	8-10	21-23	22-23	43-46	11	6	12-13	13-14	17-18	18-19
†*L. middendorfii*	8-12	21-23	21-24	42-47	10-12	5-6	10	10-11	14	15-16


†Lycopteridae
Hiodontiformes
†Lycoptera
†Tongxinichthys
†Yanbiania
†Plesiolycoptera
†Eohiodon
†H. consteniorum
Hiodon
16-23
11-15
9-10
1-8

		†Lycoptera	†Tongxinichthys	†Yanbiania	†Plesiolycoptera	†Eohiodon	†H. consteniorum	Hiodon
1	Smx	▨	▨	■	■	■	■	■
2	Dapt	▨	▨	■	■	■	■	■
3	So	▨	▨	■	■	■	■	■
4	Hmh	▨	▨	■	?	?	■	■
5	Op	▨	▨	■	?	■	■	■
6	Afq	▨	▨	■	■	■	■	■
7	Pa	▨	▨	■	?	■	■	■
8	Vfr	▨	▨	■	■	■	■	■
9	Pafr	▨	▨	▨	■	■	▨	■
10	Ap	▨	▨	▨	■	■	■	■
11	So.c	▨	▨	▨	▨	■	■	■
12	Fr	▨	▨	▨	▨	■	■	■
13	CV	▨	▨	▨	▨	■	■	■
14	Sdf	▨	▨	▨	▨	■	■	■
15	Ash	▨	▨	▨	▨	■	■	■
16	Pdpo	▨	▨	▨	▨	▨	■	■
17	Pmx	▨	▨	▨	▨	▨	■	■
18	Mcpm	▨	▨	▨	▨	▨	■	■
19	Pcv	▨	▨	▨	▨	▨	■	■
20	Npu1	▨	▨	▨	▨	▨	■	■
21	Npu2	▨	▨	▨	▨	▨	■	■
22	Na	▨	▨	▨	▨	▨	■	■

? Unknown ▨ Plesiomorphic ■ Apomorphic

FIGURE 6-8: The most parsimonious tree generated by MacClade 3.04 and PAUP 3.1.1 from the cladistic analyses of the 22 characters listed in Appendix 6-I and their distributions in Hiodontiformes. Lycopterids are here used for out group comparison purpose. Note that †*Hiodon consteniorum* sp. nov. is most closely related to the Recent *Hiodon* species.

the infraorbital series (Fig. 2A and 2-3).

A cladistic analysis of 22 characters and their states in †*H. consteniorum* and other genera of Hiodontiformes *sensu stricto* (Fig. 6-8) supports the classification of †*H. consteniorum* in *Hiodon*. All of the characters were based on the skeletal system and observable on the fossil specimens. All characters were initially assumed to be unordered. The polarity of the characters was determined by comparison with the condition in the presumed osteoglossomorph stem-group †Lycopteridae. This family, represented by two genera, is employed as the outgroup in this chapter. The analysis led to one shortest tree with a length of 23 steps and a CI of 0.96 among the known character states (Fig. 6-8).

Within the clade of Hiodontiformes *sensu stricto*, placing †*Plesiolycoptera* as sister to †*Yanbiania* increases the tree length by two steps to 25; changing the position of †*H. consteniorum* to the †*Eohiodon* clade greatly increases the tree length to 30 steps. I conclude that: 1) †*Plesiolycoptera* is more closely related to North American hiodontids than it is to †*Yanbiania*; and 2) †*H. consteniorum* is more closely related to Recent species of *Hiodon* than it is to †*Eohiodon*. This second conclusion is particularly supported by characters 16–18 and 22.

Character 16 concerns the opercle. The two Recent species of *Hiodon* have an opercle that has an acute postero-dorsal projection and a protruding upper posterior border (Fig. 6-9D). The exposed right opercle of †*H. consteniorum* sp. nov. is basically the same as that in the two Recent species of *Hiodon* in these respects (Figs. 6-3 and 6-9C). This feature is here considered to be an important synapomorphy of all species of *Hiodon*, including †*H. consteniorum*. In addition, the shape of the preopercle and subopercle in †*H. consteniorum* is almost identical to that in Recent *Hiodon*.

Character 17 describes the premaxilla. A raised anterior portion of this bone is probably plesiomorphic for all teleostean fishes; it is present both in the most primitive groups, such as pholidophoriforms and leptolepiforms (Patterson 1967, 1973, 1975, 1982; Patterson and Rosen, 1977; Arratia, 1987), and in primitive members of higher groups such as clupeomorphs (Grande 1985b; pers. obs.) and primitive euteleosts (Patterson, 1970), as well as acanthomorph fishes (Gregory, 1933; pers. obs.).

In the two Recent species of *Hiodon*, the anterior portion of the premaxilla is not raised; it is even lower than the posterior portion. †*H. consteniorum* sp. nov. has a premaxilla resembling that in the two Recent *Hiodon* species. I suggest that the lowering of the anterior portion of the premaxilla is another important synapomorphy linking †*H. consteniorum* with Recent *Hiodon*.

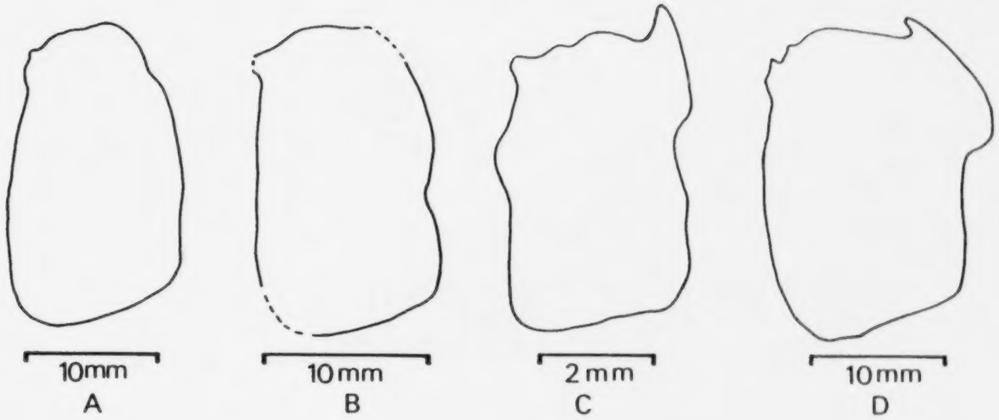


FIGURE 6-9: Diagram showing the variation of the opercle in Hiodontiformes *sensu stricto*. **A**, †*Yanbiania wangqingica*, drawn from IVPP 6767-10; **B**, †*Eohiodon rosei*, based on UALVP 12436b; **C**, †*Hiodon consteniorum* sp. nov., based on UALVP 38875; and **D**, *Hiodon alosoides*, drawn from UAMZ 6714.

Character 18 is also related to the premaxilla. A mid-dorsal concavity in this bone seems unique to *Hiodon* (pers. obs.). The only difference is that this concavity in the two Recent *Hiodon* species is broader and shallower than that in †*H. consteniorum*.

Character 22 refers to the nasal. A pair of typical curved tubular nasals can be seen in the two Recent *Hiodon* species (pers. obs.). The nasal in †*H. consteniorum* is definitely tubular and curved in shape and hardly distinguishable from that in the two Recent *Hiodon* species. This element is, however, not typical tubular and strongly curved in other hiodontids; it may be gutter-like or irregularly subrectangular in †Lycopteridae and all other osteoglossomorph fishes.

In addition, the caudal skeleton of †*H. consteniorum* is virtually identical to that in the two Recent *Hiodon* species. A potential character distinguishing the new species from the other fossil hiodontids (including †*Yanbiania*, †*Plesiolycoptera*, and †*Eohiodon*) is the double full neural spines developed on the second preural of the female allotype (Fig. 6-5). In Recent teleosts a second preural centrum bearing two full-length neural spines seems to be present only in the two Recent *Hiodon* species [pers. obs., e.g. UAMZ 3200, UAMZ 6714, *H. alosoides* (Fig. 6-6); UAMZ 4602 (radiograph) and UAMZ 4389, *H. tergisus*) (Fig. 6-7)]. Perhaps this centrum is an ontogenetic fusion of two centra. As is usual in the two Recent *Hiodon* species, the neural spine on the first preural centrum of the allotype of †*H. consteniorum* is also not developed (Fig. 6-5).

Judging from the above character analyses, †*H. consteniorum* is more closely related to the Recent *Hiodon* than it is to any other known fossil hiodontid species.

ii: Evolution of the Postcranial Skeleton in Hiodontidae

The controversy about the importance of fossil materials has been summarized recently by Grande (1985a), Wilson (1992), Wilson and Williams (1993). The fossil record of hiodontid fishes from the late Early Cretaceous †*Yanbiania* (Li, 1987) to the probable late Eocene †*H. consteniorum* is evidence to support the opinion that fossil materials provide important information on the evolution of lineages, the diversification of taxa, the biogeographic history of groups, and especially on the sequence of acquisition of derived features.

Nelson (1969), Greenwood (1970), Zhang and Zhou (1976), Patterson (1981), Li (1987), and Wilson and Williams (1992) discussed the origin of the Recent North American species of *Hiodon*. I find evidence that important evolutionary changes occurred in this family not only in the skull (e.g., opercle, Fig. 6-9), but also in the postcranial skeleton. The postcranial character states present in the Recent *Hiodon* result from at least four stages of evolution, each of which is indicated by a fossil taxon.

Stage 1: Seven-rayed Pelvic Fins– The seven-rayed pelvic fin is a fixed character state seen on all specimens of the two Recent species of *Hiodon* examined in this study (Tables 6-1 and 6-2). Tracing this character state in Hiodontidae indicates that a pair of seven-rayed pelvic fins occurred first in the late Early Cretaceous †*Yanbiania*; after this it is consistently present in all species of †*Yanbiania*, †*Plesiolycoptera* (pers. obs.), †*Eohiodon* (Cavender, 1966; Wilson, 1977, 1978; Grande, 1979), and †*H. consteniorum* (Table 6-3).

It is true that small pelvic fins are also present in other osteoglossomorphs; however, none of them includes seven rays. The genera and species most reliably referred to the Late Jurasic and Early Cretaceous †Lycopteridae, the probable stem-group of Osteoglossomorpha (see Chapters 5 and 7 in detail), possess a pair of pelvic fins mainly consisting of five or six rays (e.g., †*Lycoptera middendorffii* or †*L. davidi*, and †*Tongxinichthys*, pers. obs.). The Eocene †*Phareodus* (Osteoglossidae) possesses a pair of pelvic fins comprising six rays (pers. obs.). So does the Late Cretaceous or Paleocene †*Ostariostoma* (Schaeffer, 1949; Grande and Cavender, 1991), which may be a notopteroid (see Chapter 7). In the Recent osteoglossomorphs with pelvic fins, the fin may include six (e.g., *Osteoglossum*, *Heterotis*, and *Pantodon*) or five (e.g. *Notopterus*, *Scleropages*, and *Arapaima*) rays (Taverne, 1977, 1978; pers. obs.).

I suggest that the seven-rayed pelvic fin in Hiodontidae is more derived than the five- or six-rayed pelvic fin present in the Late Jurassic and Early Cretaceous lycopterids, in the Eocene †*Phareodus* and most of the other Recent osteoglossiforms.

Stage 2: Larger Anal Fin– The anal fin in Hiodontidae appears to have undergone a process of enlargement after the stage represented by the late Early Cretaceous †*Yanbiania*. In that genus the anal fin is almost as large as the dorsal fin (Li, 1987), which includes 11 to 12 principal rays supported by 13 to 14 anal pterygiophores. The initial stage of enlargement of the anal fin is seen in the early Late Cretaceous †*Plesiolycoptera*, which has an anal fin consisting of 20 principal rays supported by 22 anal pterygiophores (Zhang and Zhou, 1976).

In the Eocene †*Eohiodon*, the anal fin varies in size from one species to another. The type species †*E. rosei* has an anal fin composed 14 to 18 principal rays supported by 16 to 19 pterygiophores (Cavender, 1966; Wilson, 1977; pers. obs.). †*E. woodruffi* (Wilson, 1978) possesses an anal fin consisting of 18 to 19 principal rays and 20 anal pterygiophores. †*E. falcatus* (Grande, 1979) has an anal fin composed 21-24 principal rays and 21-25 anal pterygiophores, the only two character states that make this species different from †*E. woodruffi* (pers. obs., see Chapter 5).

The largest anal fin in the Hiodontidae is developed in the Recent *Hiodon alosoides*, which has 31 to 33 principal rays (Table 6-1) supported by 33 to 34 (Grande, 1979; pers. obs.) or even 36 (Cavender, 1966) anal pterygiophores.

An anal fin larger than the dorsal fin is indeed present in some other teleosts such as clupeomorphs (Grande, 1985b). Large anal fins, usually found together with large dorsal fins, are also seen in other osteoglossomorphs such as †*Phareodus* (Grande, 1984) and Recent genera. I consider these to be examples of convergence.

Stage 3: Falcate Dorsal Fin and Dimorphic Anal Fin– In †*Yanbiania* the dorsal fin is triangular but definitely not falcate in shape. Its anal fin does not show sexual dimorphism in any of the specimens (V6767) in the collection of the IVPP referred to that species (Li, 1987), nor does the anal fin in †*Plesiolycoptera* (pers. obs.). It is in the Eocene †*Eohiodon* that a falcate dorsal fin (Grande, 1979) and a sexually dimorphic anal fin can be identified (Wilson and Williams, 1993). These two character states seem to have evolved in the Hiodontidae at about the same time (by the Eocene), and continue to be present in †*H. consteniorum* (Fig. 1) and the two Recent *Hiodon* species.

In the two Recent *Hiodon* species, adult females usually have an anal fin base relatively shorter than that in males. In addition, the females mostly have a relative body depth greater than that in males (judging from the ratio of BD/SL, see Appendices 6-II to 6-V). This kind of difference between adult females and males can also be recognized in the Eocene †*Eohiodon* (pers. obs.) and in †*H. consteniorum*, possibly implying that a dimorphism in body depth had also evolved by the Eocene. However, as noted by Wilson and Williams (1993), the fossil hiodontids show sexual dimorphism at much smaller body sizes, and presumably in much younger individuals, than do the Recent species. This appears to apply also to †*H. consteniorum*, although extremely small specimens are not yet known.

Stage 4: More Vertebral Centra and Changes in the Caudal Skeleton– The number of vertebrae in *Hiodon* has been greatly increased as compared with that in the other genera of Hiodontidae (Table 6-3). In the late Early Cretaceous †*Yanbiania*, 44 to 46 vertebrae are present, with the caudals and precaudals about equal in number. †*Plesiolycoptera* has at least 41 or 42 vertebrae, of which 19 to 20 are precaudals (pers. obs.). The vertebrae in †*Eohiodon* range from 44 to 50 in different species (Wilson, 1977, 1978; Grande, 1979; pers. obs.), with precaudals usually one or two fewer than caudals (Table 6-3).

The increase of vertebral centra in Hiodontidae is first known in †*H. consteniorum*,

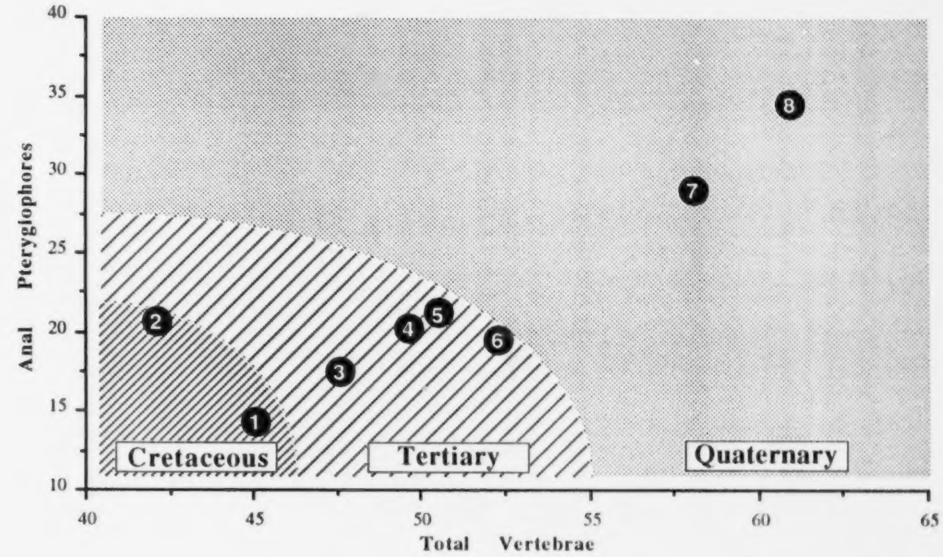


FIGURE 6-10: Diagram showing the approximately proportional relationship between the increase in the number of vertebral centra and the enlargement of the anal fin in Hiodontidae, based on data of Table 6-3. This relationship is basically consistent with the evolutionary history of the family from the Cretaceous species to the extant ones. Numbers in this graph represent the species referred to the Hiodontidae in this this chapter. **1** †*Yanbiania wangqingica*; **2** †*Plesiolycoptera daqingensis*; **3** †*Eohiodon rosei*; **4** †*Eohiodon woodruffi*; **5** †*Eohiodon falcatus*; **6** †*Hiodon consteniorum* sp. nov.; **7** *Hiodon tergisus*; **8** *Hiodon alosoides*.

which has a vertebral column consisting of at least 52 centra, 25 of them caudals. In the Recent *Hiodon* species, *H. tergisus* has a vertebral column comprising 55 to 58 centra; and *H. alosoides* 58 to 61 (Cavender, 1966; Grande, 1979) or even 63 (pers. obs.), with 25 to 28 caudals (Table 6-3).

The increase in number of vertebral centra in this family is roughly proportional to the enlargement of the anal fin from the late Early Cretaceous †*Yanbiania* to the two Recent *Hiodon* species (Fig. 6-10). This relationship is basically consistent with the phylogeny of the family.

At the same time, the structures of the caudal skeleton in *Hiodon* have also changed. Greenwood (1970) noticed the close resemblance of the caudal skeleton between the Late Jurassic-Early Cretaceous †*Lycoptera* and Recent *Hiodon*; however, his illustration for *H. tergisus* [p. 276, fig. 8, drawn from the radiograph of BM(NH) 1862] does not show all of the structures of the caudal skeleton for that species. Others (Gosline, 1960; Patterson, 1968a-b; Taverne, 1977; Schultze and Arratia, 1988, 1989) pay more attention to the last two urals and the first preural.

At least four character states in the caudal skeleton of *Hiodon* are notable here:

1. The neural spine on the first preural centrum is reduced or absent (partly agreeing with Schultze and Arratia, 1988).
2. The second preural centrum often has two full neural spines.
3. In *H. tergisus* the number of uroneurals is as few as two.
4. The parhypural has fused with the first preural centrum (agreeing with Schultze and Arratia, 1988).

The first two of these features seem especially to be phylogenetically useful.

Patterson and Rosen (1977) considered "a full neural spine on pu1" to be an important synapomorphy shared by all osteoglossomorph fishes, both fossil and Recent. However, this is not consistent with *Hiodon* (as indicated by Taverne, 1977: fig. 26; Schultze and Arratia, 1989: figs. 2, 4; and Grande and Cavender, 1991: 407). My examination of the specimens available to me reveals that the neural spine on the first preural centrum is rudimentary in the two Recent species (e.g., Fig. 6-6); it is even absent on some specimens (e.g. Fig. 6-7). A similar condition is also present in the new fossil species described in this chapter (Fig. 6-5).

A second preural centrum bearing two full neural spines can be seen in †*H. consteniorum* (Fig. 6-5), *H. alosoides* (Fig. 6-6), and *H. tergisus* (Fig. 6-7) although this feature is not present on all specimens. The same state was also present in two of the three specimens of *H. tergisus* studied by Schultze and Arratia (1988: fig. 11 A-B and

E-F, based on KU 9662).

In fossil teleosts a second preural centrum with double full neural spines has so far been recorded in the Eocene †*Phareodus testis* (Taverne, 1978: fig. 13; Grande, 1984; also see Chapter 2) and in at least one specimen of the Early Cretaceous †*Cladocyclus* (Patterson and Rosen, 1977, fig. 19: †*C.* sp.; Maisey, 1991, p. 199: †*C. gardneri* based on AMNH 9982A). A further investigation of this character state will be made before I reach conclusions about its significance to the phylogeny and evolution of osteoglossomorph fishes.

Regarding the uroneurals, some decrease or fusion of these elements has occurred in *Hiodon*. Schultze and Arratia (1988) illustrated a caudal skeleton of *H. alosoides* (p. 261, fig. 2, drawn from KU 13993) which shows only two complete uroneurals. A similar condition is also seen in some UAMZ specimens (e.g. Fig. 6-7).

CONCLUSIONS

†*Hiodon consteniorum* sp. nov. is the oldest representative of the genus *Hiodon*. Assignment of this new fossil species to the genus *Hiodon* is particularly supported by derived characters shown on the nasal, the premaxilla, and the opercular series. Characters from the palatopterygoid and hyoid arches, the infraorbitals, and from the caudal skeleton also support this relationship.

Seven-rayed pelvic fins may be a synapomorphy of all fossil and Recent Hiodontidae. In the earliest members of the Hiodontidae, the anal fin is not distinctly larger than the dorsal fin, but it is distinctly larger in most later species. A falcate dorsal fin and a sexually dimorphic anal fin appear to have evolved at approximately the same time (by the Eocene) in the history of the Hiodontidae. An increase in the number of vertebral centra, along with changes in the nasal, premaxilla, opercle, and caudal skeleton mark the origin of the Recent genus *Hiodon*.

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APPENDIX 6-I

22 characters used in cladistic analysis:

1. Supramaxilla: (Smx)
   [0] = present
   [1] = absent

2. Dorsal arm of post-temporal: (Dapt)
   [0] = less than 1.5 times as long as ventral arm
   [1] = more than twice as long as ventral arm

3. Supraorbital: (So)
   [0] = present
   [1] = absent

4. Heads of hyomandibular articulating with cranium: (Hmh)
   [0] = one
   [1] = two (they may be bridged)

5. Opercle: (Op)
   [0] = oval or kidney-shaped
   [1] = irregular parallelogram

6. Articulation facet for quadrate: (Afq)
   [0] = on angulo-articular and retroarticular
   [1] = on articular and angulo-retroarticular

7. Parietals: (Pa)
   [0] = posteriorly not separated by supraoccipital
   [1] = posteriorly separated by supraoccipital

8. Pelvic fin rays: (Vfr)
   [0] = five to six
   [1] = seven

9. Principal anal fin rays: (Pafr)
   [0] = 12-18
   [1] = 20-33

10. Anal pterygiophores: (Ap)
    [0] = 14-19
    [1] = 22-36

11. Supraorbital canal: (So.c)
    [0] = ending in posterior portion of parietal
    [1] = ending in anterior portion of parietal or in frontal

12. Frontal: (Fr)
    [0] = more than two times as long as parietal
    [1] = less than two times as long as parietal

13. Caudal vertebrae: (CV)
    [0] = fewer than 24
    [1] = 25-28

14. Shape of dorsal fin: (Sdf)
    [0] = triangular
    [1] = falcate

15. Shape of anal fin: (Ash)
    [0] = same shape in both sexes
    [1] = sexually dimorphic

16. Postero-dorsal projection of opercle: (Pdpo)
    [0] = absent
    [1] = present

17. Premaxilla: (Pmx)
    [0] = anterior portion raised
    [1] = anterior portion not raised or lower

18. Mid-dorsal concavity on premaxilla: (Mcpm)
    [0] = absent
    [1] = present

19. Precaudals: (Pcv)
    [0] = fewer than 26
    [1] = 27-33

20. Neural spine on first preural centrum: (Npu1)
    [0] = complete
    [1] = rudimentary

21. Neural spine on second preural centrum: (Npu2)
    [0] = single
    [1] = double or potential to be double

22. Nasal: (Na)
    [0] = gutter-like or irregularly subrectangular
    [1] = curved and tubular

APPENDIX 6-II: Measurements of *Hiodon alosoides* (adult) from the North Saskatchewan River, near Edmonton, Alberta.

UAMZ SPECIMENS	TL	SL	BD	HL	ML	PPL	PVL	PDL	PAL	CPL	CPD	FL	DFBL	AFBL
3 (fm)	375	307	94	61	21	38	118	196	186	32	30	340	27	90
4 (m)	369	306	85	61	20	55	121	197	186	34	27	336	25	93
3161-a (fm)	357	295	87.5	60	22	54	126	192	186	30	28	328	30	85
3161-b (m)	359	296	81	61	21	55	122	193	182	35	28	329	27	92
3161-c (m)	359	298	85	58	21	55	121	194	187	32	27.2	330	31.6	88
3161-d (m)	359	303	87	60	19.4	55	122	198	184	34	27.5	333	30	89
3161-e (fm)	373	306	90	62	21	54	126	206	196	35	27.5	340	27	85
3155 (m)	340	280	78.6	56	19	49	108	184	170	30	26.8	314	26	87
3200 (fm)	368	297	85.5	60	18	53	121	201	190	31	28.2	332	25	87
3158-a (m)	358	292	84	57	19	52	116	191	180	31	26.7	327	30	94
3158-b (m)	376	314	97	63	20	56	132	208	200	34	29	346	28	94
3158-c (m)	343	258	80.4	57	19.5	52	115	187	171	34	26.3	313	29	86
3158-d (m)	342	277	85.4	58	19.2	52	107	182	172	31	27	309	27	85
3158-e (m)	344	285	84	59	20	54	116	187	172	35	27	315	31	84
3160-a (m)	347	288	82.2	56	19	54	120	188	178	36	26.2	320	29	82.2
3160-b (m)	328	267	75.8	51	18	48	109	174	168	30	24.2	295	26	77
3160-c (m)	333	271	85.5	58	19.5	55	109	178	168	31	27.3	306	24	86
3160-d (m)	367	298	85.7	63	22	56	129	201	196	28	27.5	334	29	87
3160-e (m)	348	290	80.8	57	19	51	116	190	182	33	26.2	317	29.5	85.4
3455 (fm)	352	292	83	60	20	55	116	189	182	35	27.5	321	27	83
3543-a (m)	379	317	83	62	20	57	128	207	191	40	30	350	29	98
3543-b (fm)	367	302	93	60	20	55	122	203	185	32	30.2	337	30	90

APPENDIX 6-III: Measurements of *Hiodon alosoides* (juveniles) from Mamawi/Claire lakes, Alberta.

	UAMZ SPECIMENS	TL	SL	BD	HL	HD	PPL	PVL	PDL	PAL	CPL	CPD	DFBL	AFBL
5	*H. alosoides (m)*	100.0	83.0	25.0	18.4	14.0	17.0	35.0	54.0	49.0	9.0	8.3	8.5	23.5
6	*H. alosoides (m)*	100.0	83.0	25.0	18.4	14.0	16.0	35.0	54.0	49.0	11.0	8.1	8.5	23.5
7	*H. alosoides (m)*	94.0	77.0	23.5	16.8	13.5	15.9	32.0	51.1	45.5	10.0	8.0	7.8	21.6
8	*H. alosoides (m)*	94.0	77.0	24.2	17.2	14.2	15.9	32.0	50.0	45.0	10.0	8.0	7.8	21.6
9	*H. alosoides (fm)*	94.0	77.0	23.0	17.0	13.4	15.9	32.0	51.0	45.0	10.0	8.0	7.8	21.6
10	*H. alosoides (fm)*	87.0	70.5	21.2	15.4	13.0	15.5	30.0	45.0	41.0	8.5	7.0	7.8	20.2
11	*H. alosoides (fm)*	90.0	74.0	23.0	16.2	13.5	15.7	30.6	49.0	44.0	9.1	7.8	6.5	20.6
12	*H. alosoides (fm)*	87.0	70.4	21.5	15.9	12.5	16.0	29.8	45.2	42.0	8.0	7.1	7.6	20.0
13	*H. alosoides (fm)*	95.0	78.0	23.2	16.5	13.6	16.0	33.0	51.2	46.0	11.0	7.7	7.0	22.6
14	*H. alosoides (m)*	91.0	74.0	22.7	15.0	13.3	15.4	30.0	48.5	43.5	8.6	7.7	7.4	21.3
15	*H. alosoides (fm)*	93.0	76.0	23.5	16.8	14.0	16.0	31.7	49.8	45.8	10.5	7.9	7.0	21.0
16	*H. alosoides (fm)*	86.0	69.2	20.5	16.0	13.0	13.5	29.0	45.0	41.0	8.7	7.0	7.0	19.5
17	*H. alosoides (m)*	90.0	73.0	22.6	16.0	13.5	14.0	29.4	47.0	43.0	10.2	7.7	7.3	20.1
18	*H. alosoides (fm)*	86.5	70.5	20.4	16.0	12.6	14.0	29.0	46.0	41.3	8.5	7.4	7.5	21.0
19	*H. alosoides (m)*	81.5	66.0	19.0	15.5	12.2	15.6	28.5	43.0	39.0	7.5	6.8	6.6	18.5
20	*H. alosoides (m)*	83.0	68.0	19.3	15.0	12.3	13.5	26.5	42.7	39.0	8.0	7.8	7.1	19.7
21	*H. alosoides (m)*	81.0	66.0	19.0	15.5	12.2	14.0	27.0	42.7	39.0	7.5	6.8	6.5	18.0
22	*H. alosoides (fm)*	94.0	77.0	23.5	16.5	13.4	15.0	31.7	50.0	44.0	10.0	8.0	8.0	22.0
23	*H. alosoides (m)*	80.0	63.0	18.5	14.3	11.7	13.5	26.8	43.0	37.4	7.0	6.6	6.8	18.0
24	*H. alosoides (m)*	80.0	63.0	19.0	14.3	12.0	12.7	27.0	42.0	37.0	7.0	6.6	6.7	18.6

APPENDIX 6-IV: Measurements of *Hiodon tergisus* from the Red Deer River, near Red Deer, Alberta.

UAMZ SPECIMENS	TL	SL	BD	HL	ML	PPL	PVL	PDL	PAL	CPL	CPD	FL	DFBL	AFBL
4389 (fm)	327	267	95.3	54	14	46	115	164	177	28	29.9	298	37	72
4595 (m)	321	263	78	57	17.5	48	110	158	173	34	26.6	290	34	65
4594 (m)	324	260	79.7	54	16.5	45	108	160	173	33	26.3	289	34	64
4596 (fm)	321	260	92	57	15.6	47	115	160	175	30	26.2	288	34	68
4589 (fm)	287	233	80	51	14	45	97	141	150	28	25	260	28.4	63
4592 (m)	307	248	84.5	56	16	48	107	151	163	28	28	276	33	65
4588 (m)	277	225	77	51	15	42	95	136	150	29	24.3	251	29	58
4590 (fm)	320	255	87	54	15	42	104	156	172	26	26.6	286	32	68
4591 (fm)	276	225	77.5	47	14.8	39	94	141	151	27	24.5	250	26	56.4
4603 (m)	283	227	72	46	13	39	92	136	148	28	25	259	28	61
4593 (m)	267	215	68	50	13.5	43	101	130	143	26	23.3	239	29	54
4602 (m)	243	196	61.5	45	12	39	84	121	130	24	21.7	221	26	52

APPENDIX 6-V: Measurements of *Hiodon tergisus* from the North Saskatchewan River, near Edmonton, Alberta.

UAMZ SPECIMENS	TL	SL	BD	HL	ML	PPL	PVL	PDL	PAL	CPL	CPD	FL	DFBL	AFBL
4571 (m)	294	236	76	55	18	48	108	143	161	28	25	264	29	58
4575 (fm)	292	235	81	53	17	48	102	143	158	27	25	265	30	62
4587 (m)	271	220	70	46	16	42	100	131	146	28	23	247	28	55
4573 (fm)	286	232	78	49	17	42	99	144	152	28	25	260	30	62
4612 (m)	305	246	80	54	17	45	105	149	165	23	26	278	31	69
4577 (fm)	328	263	89	54	17	48	115	161	180	27	28	297	34	69
4583 (m)	285	230	71	52	16	44	96	141	151	25	25	260	30	62
4585 (fm)	293	238	78	54	17	43	101	144	157	25	25	268	29	64
4568 (m)	274	223	70	51	15	45	95	141	148	25	24	250	28	57
4597 (fm)	264	215	70	47	15	41	95	132	145	25	24	241	27	55
4584 (m)	324	263	81	65	15	57	119	161	175	31	27	294	35	66
4570 (m)	276	222	71	52	14	44	97	136	148	22	24	251	31	59
4576 (m)	274	223	73	50	17	42	97	134	148	27	25	250	30	58
4569 (m)	278	222	68	49	16	43	93	138	145	27	24	250	28	56
4580 (m)	273	220	68	48	16	44	94	136	144	25	24	247	27	56
4601 (m)	281	225	72	54	16	46	102	142	152	24	24	256	31	55
4581 (m)	269	218	75	52	15	44	99	135	147	23	24	247	28	56
4651 (fm)	302	246	80	52	15	47	107	147	158	30	25	272	34	67
4600 (fm)	284	232	74	54	16	47	100	142	151	26	25	259	31	63
4598 (fm)	297	245	82	53	16	45	104	145	160	30	26	272	31	63
4572 (m)	270	217	73	51	17	42	95	136	149	24	24	244	28	59
4574 (fm)	285	234	76	52	15	46	99	146	152	28	25	260	27	60
4599 (fm)	293	240	76	57	15	48	104	148	157	29	25	267	28	61
4578 (fm)	285	232	76	55	15	48	102	145	153	26	24	260	29	62
4579 (fm)	258	213	67	47	14	45	95	132	136	26	22	237	26	56
4582 (fm)	286	234	77	53	14	45	97	138	150	29	24	262	30	62
4585 (fm)	285	233	74	56	15	48	100	141	154	31	24	257	28	57

Chapter 7

PHYLOGENETIC RELATIONSHIPS AND BIOGEOGRAPHIC HISTORY OF OSTEOGLOSSOMORPHA WITH EMPHASIS ON NORTH AMERICAN TAXA

INTRODUCTION

Knowledge on the phylogeny of Osteoglossomorpha has progressed since the beginning of this century. Regan (1909) and Gregory (1933) placed all extant osteoglossomorphs in two adjacent superfamilies, Osteoglossoidea and Mormyroidea, of the Clupeiformes. Berg (1940) raised the superfamily Osteoglossoidea to a suborder Osteoglossoidei of Clupeiformes. He exluded Mormyroidea from Clupeiformes and raised the superfamily to an order, Mormyriformes. At that time, Berg recognized Lycopteroidei as one of the suborders of Clupeiformes. Gosline (1960, 1961) separated the extant hiodontids, notopterids, and osteoglossids from all other clupeiforms, which he grouped in the division Clupei, placing them in their own division, Osteoglossi. However, his conception on the systematic position of Osteoglossi was still within the order Clupeiformes. Following Berg (1940), Gosline also treated Mormyriformes as an independent order of teleosts, though he had acknowledged the close resemblance of the caudal skeleton between his Osteoglossi and Mormyriformes. In addition, he did not consider the possible relationship between Lycopteroidei (Berg, 1940) and Osteoglossi. Greenwood (1963) elevated Gosline's Osteoglossi to the order Osteoglossiformes, and also noted the possible interrelationship of his Osteoglossiformes and Mormyriformes, but he still recognized the latter as a separate order. McAllister (1968) combined Berg's (1940) Mormyriformes with Greenwood's (1963) Osteoglossiformes, recognizing only Mormyriformes as a valid name. In McAllister's classification, hiodontids were eliminated from Osteoglossiformes, placed in Hiodontoidei, a separate suborder, of Clupeiformes, as were the fishes in †Lycopteroidei.

The Osteoglossomorpha was first defined by Greenwood, Rosen, Weitzman, and Myers in 1966. In their concept, it contains two orders: the Osteoglossiformes, which consist of Osteoglossoidei (Osteoglossidae and Pantodontidae) and Notopteroidei (Notopteridae and Hiodontidae), and the Mormyriformes, which consist of Mormyridae and Gymnarchidae. Since then, Henning's "phylogenetics" (Henning, 1966) have been extensively applied to studies of fossil and extant fishes. This application has changed the criteria for assessing teleostean phylogeny from overall similarity to derived characters or character states, and has contributed greatly to the study of Osteoglossomorpha (see Nelson, 1968, 1969a-b, 1973a-b; Greenwood, 1970, 1973; Patterson and Rosen, 1977; Lauder and Liem, 1983; Arratia, 1991).

When Greenwood et al. (1966) coined the name Osteoglossomorpha, they also divided all of the Recent teleosts into three divisions and had a polyphyletic concept of the origin of the Recent teleosts. Osteoglossomorpha were considered to represent a distinct phyletic lineage derived independently from the pholidophoroid holostean level of organization (Greenwood et al., 1966: P. 349, fig. 1).

During the past two decades, there have been two main opinions on the content and extra-group relationships of Osteoglossomorpha. One was advocated by Patterson and Rosen (1977), which treated Osteoglossiformes as coextensive with the supercohort Osteoglossomorpha, and containing Osteoglossoidei and Notopteroidei. On the basis of their cladistic arrangement of teleosts, Patterson and Rosen held the concept that Osteoglossomorpha are the sister-group of all other extant teleosts. In contrast, Taverne (1979) enlarged the Osteoglossomorpha to contain Hiodontiformes, Ichthyodectiformes, Mormyriformes, and Osteoglossiformes. Taverne's scheme of Osteoglossomorpha has never been commonly accepted among paleoichthyologists because his concept about both the intra- and extra-group relationships of Osteoglossomorpha is based on similarities, most of which are primitive characters.

Recently, Arratia (1991) queried the reality of the extra-group relationships of Osteoglossomorpha asserted by Patterson and Rosen in 1977. She found, based on a cladistic analysis of 67 caudal skeletal characters, that Osteoglossomorpha are not the most primitive group, or at least not more primitive than Elopomorpha, in the teleostean lineage.

Meanwhile, controversies on intra-group relationships and historical biogeography of Osteoglossomorpha continue to puzzle vertebrate paleontologists and ichthyologists (see Nelson, 1969a, 1969b, Greenwood, 1970, 1973; Zhang and Zhou, 1976; Grande, 1985a, 1989; Gayet, 1987; Li, 1987; Wilson and Williams, 1993). These perplexing questions are all closely related to the study of the North American osteoglossomorph fishes, which, with the new taxa described in this thesis, include important representatives of most of the major clades in the group.

The purpose of this chapter is to reassess the phylogeny of the Osteoglossomorpha on the basis of the study of the new fossil osteoglossomorphs from North America and a detailed cladistic analysis of 84 characters and the distribution of their states in 40 taxa.

Comparative Materials

Besides the specimens listed in the previous chapters (Chapter 2 to 6), the following materials (including some primitive euteleosts) are also included in the study for this chapter.

Osteoglossiformes– Mormyridae: *Gnathonemus* sp., one alizarin prepared (UAMZ 6755, SL=81) and two formalin-preserved (UAMZ 6670, SL=83-110) specimens.

†Ostariostomidae: †*Ostariostoma wilseyi* Schaeffer, one specimen listed in Schaeffer (1949) and Grande and Cavender (1991).

Gonorynchiformes– Chanidae: *Chanos chanos*, one alizarin prepared specimen (UAMZ 3523, SL=93).

Salmoniformes– Osmeridae: *Hypomesus*, one alizarin prepared specimen (UAMZ 874, SL=115); *Thaleichthys*, two alizarin prepared specimens (UAMZ 3939, SL=71, 76).

Salmonidae: *Coregonus clupeiformis*, two dried skulls (UAMZ 6829).

EXTRA-GROUP RELATIONSHIPS AND SYNAPOMORPHIES OF OSTEOGLOSSOMORPHA

Greenwood (1968, 1973) suggested that Osteoglossomorpha and Clupeomorpha are sister-groups because they share a similar type of otophysic connection. Patterson and Rosen (1977), Lauder and Liem (1983), and Nelson (1994) considered Osteglossomorpha to be the sister-group of the clade consisting of Elopomorpha and Clupeomorpha plus Euteleostei. Arratia (1991) argued that elopomorphs might be more primitive than osteoglossomorphs in the structure of their caudal skeleton. Recently, I have also attempted to clarify the above controversies. For this purpose, a cladistic analysis of 84 characters (Appendix 7-I) and their states distributed in the 40 taxa included in this study (see Table 7-1A-D) has been carried out. Fig. 7-1 is the preferred shortest tree generated by MacClade 3.04; and Figs. 7-2 and 7-3 are two consensus trees produced by PAUP 3.1.1 based on the 30 most pasimonious trees with 197 steps. All three cladograms strongly support the following conclusions.

TABLE 7-1A: Data matrix showing the distribution of states of characters 1-21 of the 84 characters listed in Appendix 7-I. In total, 40 taxa are examined and included in the cladistic analysis.

CHARACTERS AND THEIR STATES	TAXA	†*Leptolepis coryphaenoides*	†*Tharsis dubius*	†*Anaethalion knorri*	Elopoidei	†*Allothrissops mesogaster*	†*Cladocyclus gardneri*	†*Lycoptera davidi*	†*Yanbiania wangingica*	†*Eohiodon rosei*	†*E. woodruffi*	†*H. consteniorum sp. nov.*	*Hiodon tergisus*	*H. alosoides*	†*Tanichthys*	†*Chandlerichthys*	†*Laeliichthys*	†*Joffrichthys gen. nov.*	†*Sinoglossus*	*Heterotis*	*Arapaima*	†*Cretophareodus gen. nov.*	†*Phareodus testis*	†*P. encaustus*	†*P. queenslandicus*	†*P.* (=†*Brychaetus*) *muelleri*	*Pantodon*	†*Singida*	*Scleropages*	*Osteoglossum*	†*Thaumaturus*	†*Ostariostoma*	Mormyroidea	*Xenomystus nigri*	*Notopterus notopterus*	*Papyrocranus afer*	Clupeoidea	Pristigasteroidea	*Chanos*	*Hypomesus*	*Coregonus*
1	Epip	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
2	Ethc	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	Gp	0	0	1	1	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	Pun	0	0	0	0	1	1	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Sec	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	0	0	?	?	?	?	?	0	?	0	0	?	?	1	1	1	1	1	1	0	0	0
6	Lpu2	0	0	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1	1	?	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7	Un	0	0	1	1	0	0	1	1	1	1	1	1	1	1	?	3	3	?	3	3	?	3	3	3	?	3	2	3	3	2	2	3	3	3	3	1	1	3	2	2
8	#H	0	0	0	1	0	0	1	1	1	1	1	1	1	2	?	2	2	?	2	2	?	2	2	?	?	2	3	2	2	1	3	3	3	3	3	2	2	3	2	2
9	Bp	0	0	?	1	0	0	1	1	1	1	1	1	1	1	?	0	1	?	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
10	Ud	0	0	0	0	0	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11	Dcs	0	0	0	0	0	1	1	1	1	1	1	1	1	1	?	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12	Nana	0	0	0	0	0	0	1	1	1	1	1	1	1	1	?	2	2	2	2	2	?	1	1	1	1	1	2	2	2	1	1	1	2	2	2	1	1	1	1	1
13	Pe-f	0	0	0	0	0	0	1	1	1	1	1	1	1	1	?	0	?	?	0	0	?	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1
14	So.c	0	0	0	0	0	0	0	0	1	1	1	1	1	0	?	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1
15	Ep	0	0	0	0	0	0	1	1	1	1	1	1	1	1	?	1	1	?	1	1	?	1	1	1	?	1	1	1	1	1	1	1	2	2	2	0	0	1	0	0
16	Smx	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1	0	0
17	Vfr	0	0	0	0	0	0	2	1	1	1	1	1	1	2	?	2	2	2	2	2	2	2	2	2	?	2	2	2	2	2	2	2	2	2	2	2	2	0	0	0
18	So	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
19	Pbm	0	0	0	0	0	0	1	1	1	1	1	1	1	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
20	Cfr	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	?	2	2	2	?	2	2	2	2	2	2	2	2	2	2	0	0	0	0	0
21	Tbhb	?	?	?	0	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	1	?	?	?	?	?	1	?	1	1	?	?	1	1	1	1	0	0	0	0	0

TABLE 7-1B: Data matrix showing the distribution of states of characters 22-42 of the 84 characters listed in Appendix 7-I. In total, 40 taxa are examined and included in the cladistic analysis.

CHARACTERS AND THEIR STATES	TAXA	*†Leptolepis coryphaenoides*	*†Tharsis dubius*	*†Anaethalion knorri*	**Elopoidei**	*†Allothrissops mesogaster*	*†Cladocyclus gardneri*	*†Lycoptera davidi*	*†Yanbiania wangingica*	*†Eohiodon rosei*	*†E. woodruffi*	*†H. consteniorum sp. nov.*	*Hiodon tergisus*	*H. alosoides*	*†Tanichthys*	*†Chandlerichthys*	*†Laeliichthys*	*†Joffrichthys gen. nov.*	*†Sinoglossus*	*Heterotis*	*Arapaima*	*†Cretophareodus gen. nov.*	*†Phareodus testis*	*†P. encaustus*	*†P. queenslandicus*	*†P. (=†Brychaetus) muelleri*	*Pantodon*	*†Singida*	*Scleropages*	*Osteoglossum*	*†Thaumaturus*	*†Ostariostoma*	**Mormyroidea**	*Xenomystus nigri*	*Notopterus notopterus*	*Papyrocranus afer*	**Clupeoidea**	**Pristigasteroidea**	*Chanos*	*Hypomesus*	*Coregonus*
22	Int	?	?	?	0	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1	1	?	?	?	?	?	1	?	1	1	?	?	1	1	1	1	0	0	0	0	0
23	Op	0	0	0	0	0	0	2	1	1	1	1	1	1	2	?	2	2	2	2	2	3	3	3	3	3	3	3	3	3	2	0	0	4	4	4	0	0	0	0	0
24	Io4-5	0	0	0	0	0	0	0	?	1	1	1	1	1	1	?	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
25	Fl/Pl	0	0	0	0	0	0	0	0	1	1	1	1	1	1	?	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	0	0
26	Na	0	0	0	0	0	0	0	0	0	0	1	1	1	2	?	2	2	2	2	2	?	2	2	2	2	2	2	2	2	0	2	2	2	2	2	0	0	0	0	0
27	U2-h	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	?	1	1	?	0	0	0	?	1	0	1	1	0	0	1	1	1	1	0	0	0	0	0
28	Pomc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0
29	Nu1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1	?	1	1	?	2	2	?	?	1	1	1	1	1	0	0	0	1	1	0	0	0	0	0
30	Io2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	?	2	2	2	2	2	0	0	0	?	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
31	Dsh	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	?	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0
32	Prda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	?	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0
33	P-qa	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
34	Paec	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	1	?	1	1	1	?	1	?	1	1	?	0	0	1	1	1	0	0	0	0	0
35	Dapt	0	0	?	0	0	0	0	1	1	1	1	1	1	0	?	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
36	Hmh	0	0	0	0	0	0	0	2	1	1	2	2	2	0	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	Sdsp	0	0	0	0	0	0	0	1	1	1	1	1	1	0	?	0	?	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
38	CKW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	Sca	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	1	1	1	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
40	Lvap	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0
41	Hap	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
42	Bhbb	?	?	?	0	0	0	0	0	0	0	0	0	0	?	?	?	0	?	0	0	?	1	1	?	?	1	?	1	1	1	?	1	0	0	0	0	0	0	0	0

TABLE 7-1C: Data matrix showing the distribution of states of characters 43-63 of the 84 characters listed in Appendix 7-I. In total, 40 taxa are examined and included in the cladistic analysis.

TAXA CHARACTERS AND THEIR STATES		*†Leptolepis coryphaenoides*	*†Tharsis dubius*	*†Anaethalion knorri*	**Elopoidei**	*†Allothrissops mesogaster*	*†Cladocyclus gardneri*	*†Lycoptera davidi*	*†Yanbiania wangingica*	*†Eohiodon rosei*	*†E. woodruffi*	*†H. consteniorum sp. nov.*	*Hiodon tergisus*	*H. alosoides*	*†Tanichthys*	*†Chandlerichthys*	*†Laeliichthys*	*†Joffrichthys gen. nov.*	*†Sinoglossus*	*Heterotis*	*Arapaima*	*†Cretophareodus gen. nov.*	*†Phareodus testis*	*†P. encaustus*	*†P. queenslandicus*	*†P. (=†Brychaetus) muelleri*	*Pantodon*	*†Singida*	*Scleropages*	*Osteoglossum*	*†Thaumaturus*	*†Ostariostoma*	**Mormyroidea**	*Xenomystus nigri*	*Notopterus notopterus*	*Papyrocranus afer*	**Clupeoidea**	**Pristigasteroidea**	*Chanos*	*Hypomesus*	*Coregonus*
43	Pena	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	?	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0
44	Pfr1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0
45	Ja	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	2	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0
46	Fr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	1	2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
47	Rdwo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	Ses	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	Pop	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	Hm	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	Sio3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	2	2	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
52	IOL	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
53	Ioc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	1	0
54	Utr	?	?	?	0	?	?	?	?	?	?	?	0	0	?	?	?	?	?	0	0	?	?	?	?	?	0	?	0	0	?	?	1	1	1	1	0	0	0	0	0
55	Mc	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0
56	Ash	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	Pmx	0	0	0	0	0	0	0	0	0	1	2	2	2	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
58	Pdpo	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	Mcpm	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	BK	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
61	Npu1	0	0	0	0	0	0	0	0	0	0	1	1	1	0	?	0	0	?	0	0	?	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2
62	#Npu2	0	0	0	0	0	1	0	0	0	0	1	1	1	0	?	0	1	?	0	0	?	1	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
63	Pemx	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 7-1D: Data matrix showing the distribution of states of characters 64-84 of the 84 characters listed in Appendix 7-I. In total, 40 taxa are examined and included in the cladistic analysis.

CHARACTERS AND THEIR STATES	TAXA	*†Leptolepis coryphaenoides*	*†Tharsis dubius*	*†Anaethalion knorri*	**Elopoidei**	*†Allothrissops mesogaster*	*†Cladocyclus gardneri*	*†Lycoptera davidi*	*†Yanbiania wangingica*	*†Eohiodon rosei*	*†E. woodruffi*	*†H. consteniorum sp. nov.*	*Hiodon tergisus*	*H. alosoides*	*†Tanichthys*	*†Chandlerichthys*	*†Laeliichthys*	*†Joffrichthys gen. nov.*	*†Sinoglossus*	*Heterotis*	*Arapaima*	*†Cretophareodus gen. nov.*	*†Phareodus testis*	*†P. encaustus*	*†P. queenslandicus*	*†P. (=†Brychaetus) muelleri*	*Pantodon*	*†Singida*	*Scleropages*	*Osteoglossum*	*†Thaumaturus*	*†Ostariostoma*	**Mormyroidea**	*Xenomystus nigri*	*Notopterus notopterus*	*Papyrocranus afer*	**Clupeoidea**	**Pristigasteroidea**	*Chanos*	*Hypomesus*	*Coregonus*
64	Aiol	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	Bhtp	?	?	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	?	1	1	?	0	0	?	?	0	?	0	0	0	?	0	0	0	0	0	0	0	0	0
66	Apop	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
67	Pmop	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
68	Osh	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
69	MB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
70	Scsc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	0	0	0	0	0	0	0	0	?	0	1	1	1	1	1	1	0	0	0
71	Mdc	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	1	0
72	Sop	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0
73	Bpcv	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0
74	SN	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
75	Abs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
76	Peaf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0
77	Fcv	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
78	Ust	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
79	Recl	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	0	0	1	1	0	0	0
80	H2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
81	Temg	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
82	Ctes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
83	St	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
84	Adf	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1

i. Sister-group Relationship between Osteoglossomorpha and the Clade Clupeomorpha plus Euteleostei

This first conclusion agrees with Arratia's (1991) suggestion about the extra-group relationship of Osteoglossomorpha; that is, osteoglossomorphs are not more primitive than elopomorphs. Osteologically, elopomorphs display a number of plesiomorphies, such as 10 [0] (the presence of urodermals), 11[0] (the presence of upper caudal scutes), 12[0] (nasals separated by the anterior portion of the frontals), 15[0] (presence of supraorbital), 16[0] (epurals as many as three), and 17[0] (presence of more than one supramaxilla). In contrast, osteoglossomorphs share all the derived states of these plesiomorphies with higher teleosts.

In all 30 shortest trees, elopomorphs and †*Anaethalion* form a clade that is linked by two synapomorphies (2[1], presence of ethmoid commissure; and 3[1], presence of a large gular plate) and one homoplasy (7[1], presence of four uroneurals) (Table 7-1A).

In the strict consensus tree (Fig. 7-2), the elopomorph-†*Anaethalion* clade lies in a polychotomy with †*Leptolepis coryphaenoides*, †*Tharsis dubius*, †*Allothrissops mesogaster*, †*Cladocyclus gardneri*, and the clade consisting of Osteoglossomorpha, Clupeomorpha, and Euteleostei.

In the 50% majority rule consensus tree (Fig. 7-3), the elopomorph-†*Anaethalion* clade is the sister-group of the clade containing †*Allothrissops mesogaster*, †*Cladocyclus gardneri*, Osteoglossomorpha, Clupeomorpha, and primitive euteleosts because they share one synapomorphy (6[1], neural spine on pu2 as long as that on pu3).

Ichthyodectiformes, represented here by †*Cladocyclus*, have been considered to belong to Osteoglossomorpha (Taverne, 1979; Nelson, 1994). In the present study they are, however, eliminated from Osteoglossomorpha (Figs. 7-1 to 7-3), taking the position of the possible sister-group of the clade consisting of Osteoglossomorpha and Clupeomorpha plus Euteleostei. The relationship among Ichthyodectiformes (†*Cladocyclus*), Osteoglossomorpha, and clupeomorphs plus euteleosts is supported by two synapomorphies (10[1], absence of urodermals from caudal skeleton, and 11[1], lost of dorsal caudal scutes).

As shown in Figs. 7-1 to 7-3, Osteoglossomorpha occupy the position of the sister-group of Clupeomorpha plus Euteleostei. This relationship is supported by one synapomorphy (12[1], anterior porton of frontal does not take part in the formation of the separation between the two nasals) and two slightly homoplastic characters (7[1/2/3], uroneurals decrease from four to zero; 8[1/2/3], hypurals decrease from seven to five or fewer).

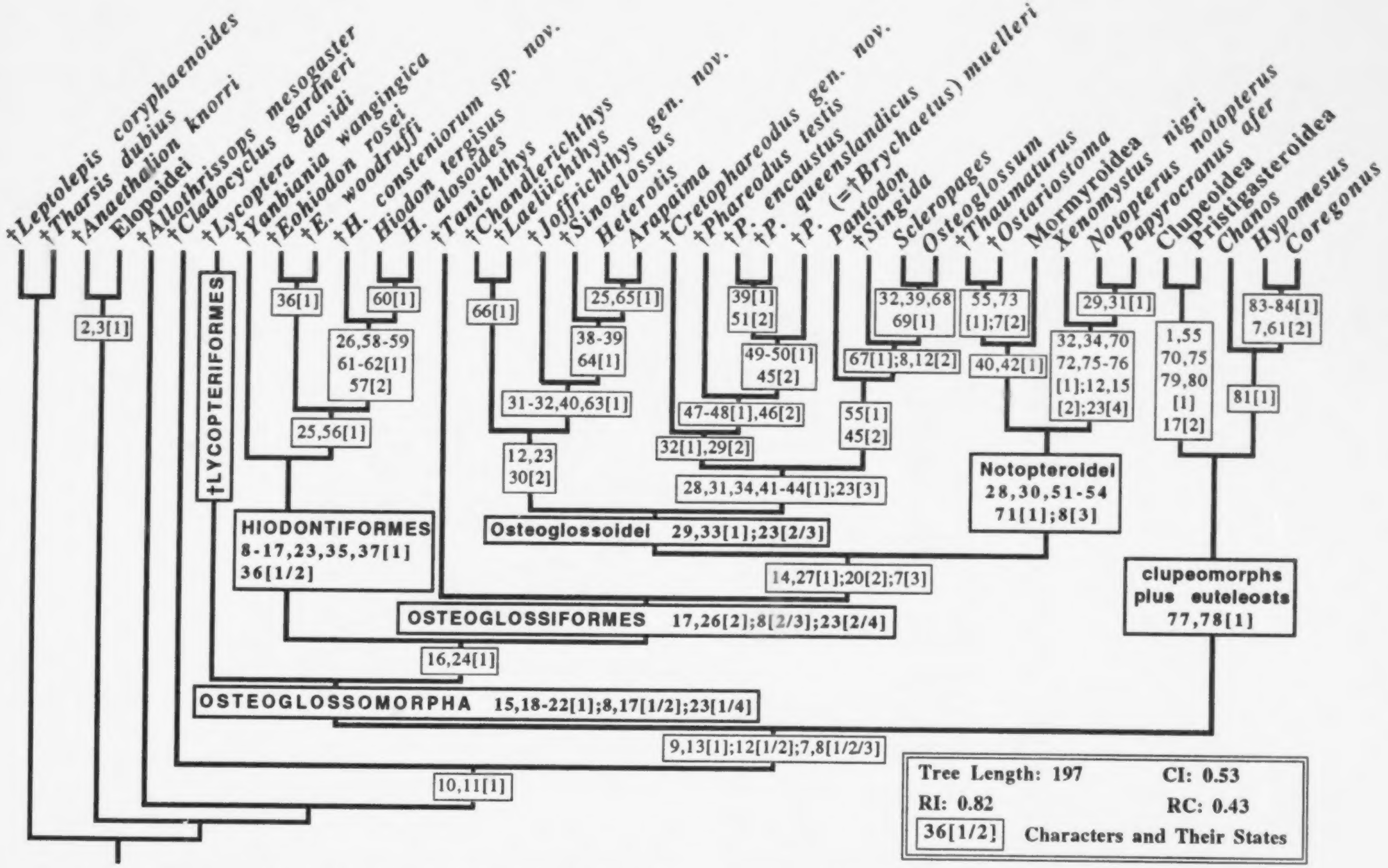

†Leptolepis coryphaenoides
†Tharsis dubius
†Anaethalion knorri
Elopoidei
†Allothrissops mesogaster
†Cladocyclus gardneri
†Lycoptera davidi
†Yanbiania wangingica
†Eohiodon rosei
†E. woodruffi
†H. consteniorum sp. nov.
Hiodon tergisus
H. alosoides
†Tanichthys
†Chandlerichthys
†Laeliichthys
†Joffrichthys gen. nov.
†Sinoglossus
Heterotis
Arapaima
†Cretophareodus gen. nov.
†Phareodus testis
†P. encaustus
†P. queenslandicus
†P. (=†Brychaetus) muelleri
Pantodon
†Singida
Scleropages
Osteoglossum
†Thaumaturus
†Ostariostoma
Mormyroidea
Xenomystus nigri
Notopterus notopterus
Papyrocranus afer
Clupeoidea
Pristigasteroidea
Chanos
Hypomesus
Coregonus
2,3[1]
36[1]
60[1]
26,58-59 61-62[1] 57[2]
25,56[1]
†LYCOPTERIFORMES
HIODONTIFORMES 8-17,23,35,37[1] 36[1/2]
66[1]
25,65[1]
38-39 64[1]
31-32,40,63[1]
12,23 30[2]
39[1] 51[2]
49-50[1] 45[2]
47-48[1],46[2]
32[1],29[2]
32,39,68 69[1]
67[1];8,12[2]
55[1] 45[2]
28,31,34,41-44[1];23[3]
Osteoglossoidei 29,33[1];23[2/3]
55,73 [1];7[2]
40,42[1]
29,31[1]
32,34,70 72,75-76 [1];12,15 [2];23[4]
Notopteroidei 28,30,51-54 71[1];8[3]
14,27[1];20[2];7[3]
OSTEOGLOSSIFORMES 17,26[2];8[2/3];23[2/4]
16,24[1]
OSTEOGLOSSOMORPHA 15,18-22[1];8,17[1/2];23[1/4]
1,55 70,75 79,80 [1] 17[2]
83-84[1] 7,61[2]
81[1]
clupeomorphs plus euteleosts 77,78[1]
9,13[1];12[1/2];7,8[1/2/3]
10,11[1]
Tree Length: 197
CI: 0.53
RI: 0.82
RC: 0.43
36[1/2] Characters and Their States

FIGURE 7-1: Preferred shortest tree showing the monophyly of Osteoglossomorpha and the possible relationships among osteoglossomorphs and other teleosts. Characters and their states (in square blackets) are listed in Appendix 7-I and Table 7-1A-D.

Although the evidence on this question is admittedly slight, I accept the concept that osteoglossomorphs are more closely related to clupeomorphs plus euteleosts than elopomorphs are to those higher taxa.

ii. Monophyly of Osteoglossomorpha

An essential point of a natural classification is to define monophyletic groups (Hennig, 1966; Wiley et al., 1991). Patterson and Rosen (1977) believed that Osteoglossomorpha were a definable monophyletic group. Recently, Shen (1993) has expressed doubt about the monophyly of Osteoglossomorpha. It seems to me that she does not have sufficient evidence to support her conclusion, based on study of the so-called "osteoglossomorphs" from China. According to Mayr and Ashlock's (1991) recent definition of monophyly, all species, including their ancestors, in a monophyletic taxon should be theoretically derived from the most recent common ancestral species which is also included in the taxon. I believe Shen was unable to support a monophyletic Osteoglossomorpha because she included some misidentified taxa in her Osteoglossomorpha, such as †*Changichthys* Su 1991, †*Suziichthys* Su 1992, and †*Nieerkunia* Su 1992, all of which may be referred to leptolepidids or even more primitive clades of teleosts.

A basic point to determine whether a given taxon is monophyletic or not is to correctly identify synapomorphies for that taxon. Greenwood et al. (1966: 351, 361-366) proposed a series of specializations for Osteoglossomorpha, but they based their hypothesis mainly on two "group characters" when they recognized Osteoglossomorpha as a distinct phyletic line of teleosts: 1) the primary bite between the parasphenoid and the tongue (=character 19[1]), and 2) the development of paired tendon bones on the 2nd hypobranchial or 2nd hypobranchial and basibranchial (=character 21[1]). These two "group characters" are still applicable today for supporting the monophyly of Osteoglossomorpha since they are not seen in other taxa (see Table 7-1A).

Patterson and Rosen (1977) defined four diagnostic features for their Osteoglossomorpha: 1) a caudal fin containing 18 principal rays, 2) a full neural spine on pu1, 3) a large postero-ventral infraorbital bone representing the third and fourth infraorbitals of other teleosts, and 4) a gut coiled so that the intestine passes to the left of the stomach. Shen et al. (1991) denied the validity of 1) and 2) as diagnostic of Osteoglossomorpha. My examination of the four characters indicates that the number of principal caudal fin rays has three relevant states. State1: caudal fin consists of 19 or more principal rays. This state is present in all the relevant out-group taxa but not in

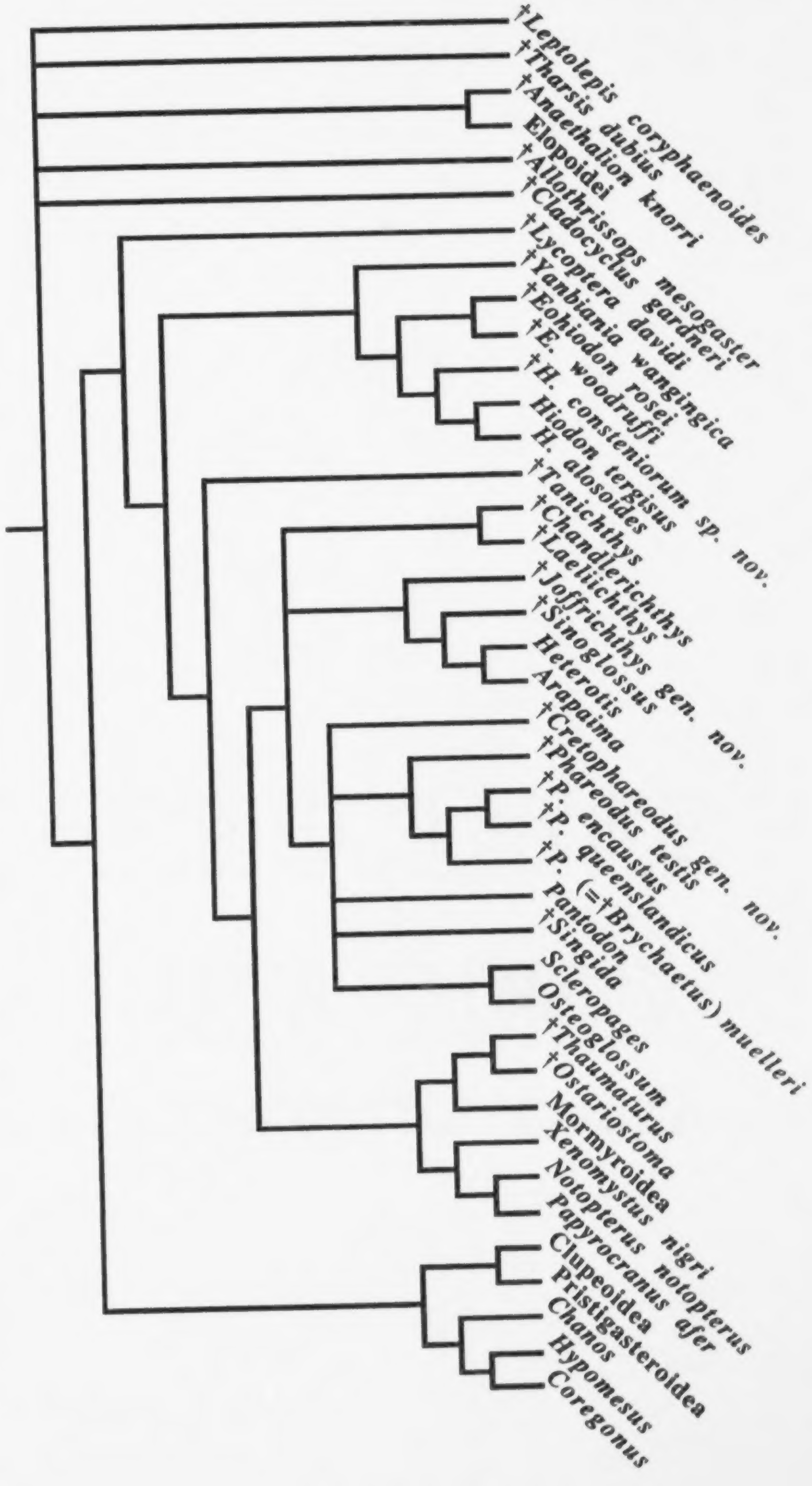

†Leptolepis coryphaenoides
†Tharsis dubius
†Anaethalion knorri
Elopoidei
†Allothrissops mesogaster
†Cladocyclus gardneri
†Lycoptera davidi
†Yanbiania wangingica
†Eohiodon rosei
†E. woodruffi
†H. consteniorum sp. nov.
Hiodon tergisus
H. alosoides
†Tanichthys
†Chandlerichthys
†Laeliichthys
†Joffrichthys gen. nov.
†Sinoglossus
Heterotis
Arapaima
†Cretophareodus gen. nov.
†Phareodus testis
†P. encaustus
†P. queenslandicus
†P. (=†Brychaetus) muelleri
Pantodon
†Singida
Scleropages
Osteoglossum
†Thaumaturus
†Ostariostoma
Mormyroidea
Xenomystus nigri
Notopterus notopterus
Papyrocranus afer
Clupeoidea
Pristigasteroidea
Chanos
Hypomesus
Coregonus

FIGURE 7-2: Strict consensus tree generated by PAUP 3.1.1 based on 30 most parsimonious trees with 197 steps. As in Fig. 7-1, this tree also suggests the monophyly of the clade Osteoglossomorpha and its sister group relationship with clupeomorphs plus euteleosts.

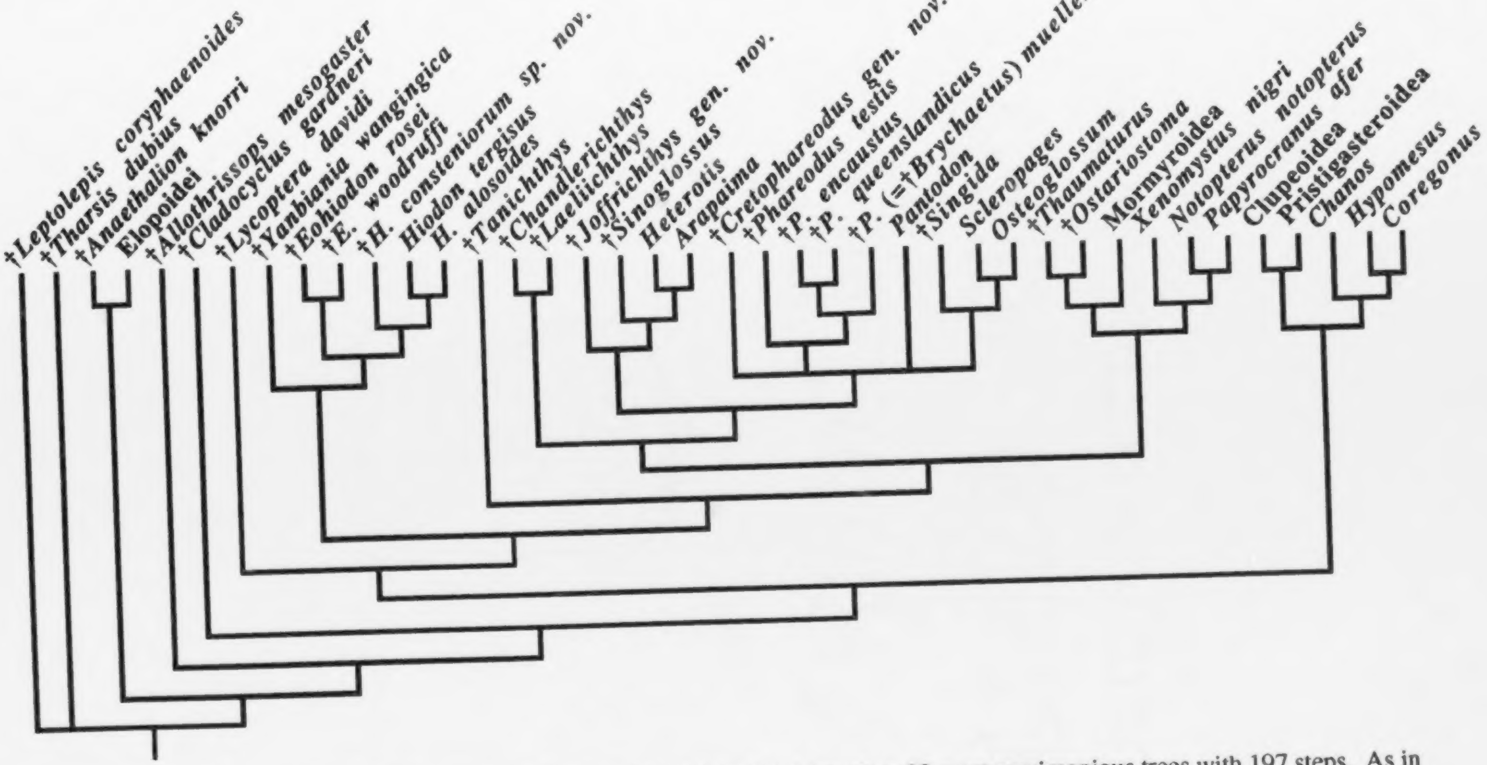

†Leptolepis coryphaenoides
†Tharsis dubius
†Anaethalion knorri
Elopoidei
†Allothrissops mesogaster
†Cladocyclus gardneri
†Lycoptera davidi
†Yanbiania wangingica
†Eohiodon rosei
†E. woodruffi
†H. consteniorum sp. nov.
Hiodon tergisus
H. alosoides
†Tanichthys
†Chandlerichthys
†Laeliichthys
†Joffrichthys gen. nov.
†Sinoglossus
Heterotis
Arapaima
†Cretophareodus gen. nov.
†Phareodus testis
†P. encaustus
†P. queenslandicus
†P. (=†Brychaetus) muelleri
Pantodon
†Singida
Scleropages
Osteoglossum
†Thaumaturus
†Ostariostoma
Mormyroidea
Xenomystus nigri
Notopterus notopterus
Papyrocranus afer
Clupeoidea
Pristigasteroidea
Chanos
Hypomesus
Coregonus

FIGURE 7-3: 50% majority rule consensus tree generated by PAUP 3.1.1 based on 30 most parsimonious trees with 197 steps. As in Figs. 7-1 and 7-2, this tree also supports the monophyly of the clade Osteoglossomorpha and its sister group relationship with clupeomorphs plus euteleosts. In addition, it suggests a basal position for elopomorphs within the Teleostei.

Osteoglossomorpha. State 2: caudal fin consists of 18 principal rays. This state is present in †*Lycoptera*, Hiodontidae, †*Tanichthys*, and Mormyridae. State 3: caudal fin consists of 17 or fewer principal rays. This third state is present in all osteoglossids, notopterids, †*Ostariostoma*, and †*Thaumaturus*. It is, thus, evident that there is a range of variation of 18 to 17 or fewer principal caudal fin rays among osteoglossomorphs. Since this range of principal caudal fin rays is not present in the out-group taxa included in this study (see character 20 in Table 7-1A), it is considered to be a valid meristic character supporting the monophyly of Osteoglossomorpha.

The neural spine on pu1 (character 61 in this paper) also has three states in the 40 taxa included in the present study (Table 7-1C). A full neural spine on pu1 (61[0]) is developed in almost all the taxa except for *Hiodon* and the primitive euteleosts examined for this study. The neural spine on pu1 in the three North American *Hiodon* species is rudimentary when it is present (61[1]) (also see Chapter 6). Thus, a full neural spine on pu1 is not a synapomophy of Osteoglossomorpha.

The so-called "large postero-ventral infraorbital bone representing the third and fourth infraorbitals of other teleosts" is a questionable character. An examination of this bone in the 40 taxa indicates that the large postero-ventral infraorbital represents the 3rd infraorbital that may be fused with io2 (e.g, †*Phareodus testis*) but not with io4. Apart from Osteoglossomorpha, such a large postero-vental 3rd infraorbital is also present in †*Anaethalion* (see Arratia, 1987), †*Cladocyclus* (see Maisey, 1991), Elopomorpha (see Forey, 1973a-b), and in *Chanos* (see Gregory, 1933, and pers. obs.). It is, thus, a teleostean plesiomorphy that does not support the monophyly of Osteoglossomorpha (see 51[0] in Table 7-1C).

Although the character state "intestine passes to the left of the stomach" can be tested only in the extant taxa, it is apparently a synapomorphy of the Recent Osteoglossomorpha (Nelson, 1972b) because none of the other extant teleostean groups shares this character state (see 22[1] in Table 7-1B).

To sum up, four of the previously defined diagnostics of Osteoglossomorpha (the two "group characters" of Greenwood et al., plus Patterson and Rosen's left-coiled intestine and 18 or fewer principal caudal fin rays) are thought to be valid synapomorphies in determining the monophyly of Osteoglossomorpha. In addition, my cladistic analysis yields at least another four osteoglossomorph synapomorphies.

a. *15[1/2], number of epurals decreased to one or zero.* As shown in Table 7-1A, the number of epurals has three states. All of the outgroup taxa, except *Chanos*, share at least two epurals (15[0]). However, most osteoglossomorphs (including hiodontids, osteoglossids, mormyroids, †*Ostariostoma*, and †*Thaumaturus*) have only one epural (15[1]). Notopterids even do not have any epural in their caudal skeleton (15[2]). Since the range of 1-0 of epural is present only in Osteoglossomorpha (and *Chanos*), it is here considered to be another important meristic synapomorphy of this superorder.

b. *16[1], absence of supramaxilla.* One or two supramaxilla are present in all the outgroup taxa. This bone is, however, not seen in all osteoglossomorphs except for †*Lycoptera* (see Table 7-1A).

c. *18[1], absence of supraorbital.* A supraorbital bone is widely present in early teleosts (Nybelin, 1974; Patterson and Rosen, 1977; Arratia, 1987), elopomorphs (Forey, 1973a-b), clupeomorphs (Grande, 1985b), and even in euteleosts (see Gregory, 1933; Patterson, 1970a; pers. obs.). It is, however, absent in all osteoglossomorphs. Ma (1987) recognized a supraorbital in †*Lycoptera*. My examination of the specimens of †*Lycoptera* failed to identify that bone. Gaudant (1968) and Greenwood (1970) also did not find a supraorbital in their lycopterid materials. The absence of a supraorbital is, thus, a unique character state of Osteoglossomorpha (Table 7-1A).

d. *24[1], io4 fused with io5.* In all the out-group taxa, io4 and io5 are separate one from another. They are, however, fused with each other in all the typical osteoglossomorphs except for †*Laeliichthys* (see Table 7-1B). Since †*Laeliichthys* is the only ingroup taxon having a separate io4 and io5 (probably secondary), the fusion of io4 with io5 is considered to be another unique character state of Osteoglossomorpha.

In total, the monophyly of Osteoglossomorpha is supported by at least eight synapomorphies. These synapomorphies are arranged in my data matrix as follows: 15[1/2], number of epurals decreased to one or zero; 16[1], absence of supramaxilla; 18[1], absence of supraorbital; 19[1], presence of primary bite of mouth between parasphenoid and basihyal; 20 [1/2], 16 or fewer principal branched caudal fin rays; 21[1], development of paired tendon bones on 2nd hypobranchial or 2nd hypobranchial and basibranchial; 22[1], intestine coiling to left of esophagus and stomach; and 24[1], fusion of io4 with io5.

COMPOSITION AND INTERORDINAL RELATIONSHIPS OF OSTEOGLOSSOMORPHA

Before I discuss the phylogeny of the North American osteoglossomorphs, there is a need to clarify the composition of Osteoglossomorpha. The original concept of Osteoglossomorpha held by Greenwood et al. (1966) contained Osteoglossiformes, which consisted of Osteoglossoidei (Osteoglosssidae and Pantodontidae) and Notopteroidei (Hiodontidae and Notopteridae), and Mormyriformes, which consisted of Mormyridae and Gymnarchidae. In 1967, Greenwood and Patterson named a fossil family †Singididae and included it in the suborder Osteoglossoidei. Later, Greenwood (1970) demonstrated a relationship between the eastern Asian lycopterids and the North American hiodontids; he then added the fossil family †Lycopteridae to Notopteroidei. Latter still, Greenwood (1973) abolished the order Mormyriformes after he reassessed the relationship among Notopteridae, Mormyridae, and Gymnarchidae. He placed all three families in the superfamily Notopteroidea.

Patterson and Rosen's (1977) Osteoglossomorpha contained only Osteoglossiformes consisting of Osteoglossoidei and Notopteroidei. They appear to have included mormyrids in their Notopteroidei.

Taverne (1979) greatly enlarged the content of Osteoglossomorpha to contain: Hiodontiformes, consisting of †Lycopteridae and Hiodontidae; †Ichthyodectiformes, consisting of †Ichthyodectidae and †Saurocephalidae; Mormyriformes, consisting of Mormyroidei (Mormyridae and Gymnarchidae) and Notopteroidei (Notopteridae); and Osteoglossiformes, consisting of Osteoglossidae, Pantodontidae, Arapaimidae, †Singididae, and †Kipalaichthyidae.

Lauder and Liem's (1983) Osteoglossomorpha was similar to Patterson and Rosen's, containing only Osteoglossiformes and consisting of Osteoglossoidei and Notopteroidei. The only difference is that Lauder and Liem explicitly included Mormyridae in their Notopteroidei.

Nelson's (1994) Osteoglossomorpha consists of †Ichthyodectiformes (containing †Allothrissopidae, †Occithrissopidae, †Cladocyclidae, †Saurodontidae, and †Ichthyodectidae) and Osteoglossiformes (containing Osteoglossoidei and Notopteroidei).

The composition of Osteoglossomorpha in this thesis is different from all of the above schemes. As used here the group contains †Lycopteriformes (†Lycopteridae), Hiodontiformes *sensu stricto* (Hiodontidae), and Osteoglossiformes, consisting of Osteoglossoidei (Osteoglossidae including Osteoglossinae and Heterotidinae) and Notopteroidei (containing at least Mormyroidea, Notopteridae, and †Ostariostomidae). The interrelationships among these three orders are stated as follows.

i. Stem-group Relationship between †Lycopteriformes and all Other Osteoglossomorphs

The establishment of the relationship between †*Lycoptera* and osteoglossomorphs has undergone a long period of study. When Müller (1847) coined the name †*Lycoptera*, he provisionally classified it as a genus of Esocidae. Woodward (1901) transferred †*Lycoptera* from Esocidae to †Leptolepidae based on the opercular elements being similar to those of leptolepids. Persons continuing use this scheme were Saito (1936), Arambourg and Bertin (1958), and Romer (1966).

In 1925, Cockerell moved †*Lycoptera* from the family †Leptolepidae and created the family †Lycopteridae according to the characters from scales. He found that tha scale of †*Lycoptera* was "practically identical with that of the European minnow, *Phoxinus phoxinus*," and then suggested that †*Lycoptera* must be "the ancestor of the Cyprinidae and their allies." Followers of Cockerell were Hussakof (1932) and Gregory (1933).

Berg (1940, 1948) grouped Lycopteridae in Clupeiformes and made it suborder Lycopteroidei of that order. Berg's scheme was based mainly on the presence of the gular plate (possibly a misidentified character of †*Lycoptera*, pers. obs.) and the absence of a Weberian apparatus in †*Lycoptera*. Berg's classification of †*Lycoptera* in Clupeiformes was adopted by Takai (1943), Liu et al. (1963), Lehman (1966), Gaudant (1968) and Mcallister (1968).

Since the 1960's, a new tendency has occurred in the study of †*Lycoptera*. This new tendency has paid attention to possible relationship between †*Lycoptera* and the Recent osteoglossomorphs. Yakovlev (1965) first noted that "......the modern teleosts most closely resembling †*Lycoptera* are the Osteoglossidae, in particular, *Arapaima......*" on the basis of the comparison of the parietal, the nasal, the hyomandibular, the basipterygoid articulation, and the bite between parasphenoid and basihyal. However, Yakovlev's hypothesis about the relationship between †*Lycoptera* and *Arapaima* has never been commonly accepted because his †Lycopteridae was a polyphyletic group that contained †*Manchurichthys* Saito 1936, †*Sinolycoptera* Yakovlev 1965 (named on the basis of †*Anaethalion langshanensis* Su 1963), and even the genus †*Mesoclupea* Ping and Yen 1933 (see Chang, 1963). According to Chang and Liu (1977), †*Manchurichthys,* as well as †*Sungarichthys* (Takai, 1943), might be primitive representatives of the Euteleostei, while †*Mesoclupea* should be grouped in the family Chirocentridae (Chang, 1963, Chang and Chou, 1977). †*Anaethalion* was considered to be related with all of the recent teleostean groups except Osteoglossomorpha (Patterson and Rosen, 1977), but is here thought to be more closely related to elopomorphs than it is to other teleostean groups (this chapter).

Greenwood (1970) suggested, after comparing the characteristics shared by †*Lycoptera* and *Hiodon*, that the idea that "......†*Lycoptera* is a member of the Osteoglossomorpha seems certain......," but he did not agree with Yakovlev's relationship between †*Lycoptera* and *Arapaima*. In Greenwood's view, most of the features used by Yakovlev to establish the relationship between †*Lycoptera* and *Arapaima* are "primitive features found in all basal teleosts." From the caudal skeleton, the number of caudal fin rays, the presence of a temporal fenestra and the details of the hyoid arch, Greenwood believed that †*Lycoptera* is more closely related to Hiodontidae than it is to any other group of teleosts. He then suggested placing Lycopteridae and Hiodontidae in one superfamily, the Hiodontoidea, which was grouped in the Notopteroidei with the Notopteroidea. Greenwood's suggestion was accepted by Zhang and Zhou (1976), Ma (1980), Patterson (1981a), Patterson and Rosen (1977), Lauder and Liem (1983), and Nelson (1994).

A comparison of †*Lycoptera* with other osteoglossomorphs suggests that the closest relationship between lycopterids and hiodontids is not valid (see Figs. 7-1 to 7-3). The characters used by Greenwood to link lycopterids with hiodontids are either plesiomorphic in Osteoglossomorpha (e.g., one epural, which is commonly seen in osteoglossomorphs, pers. obs.) or highly homoplastic (e.g., seven hypurals, which is also present in some elopomorphs; see Forey, 1973b).

The phylogenetic significance of the "temporal fenestra" in both lycopterids and hiodontids needs to be clarified. This opening was first noted to be present in hiodontids by Ridewood (1904) and in lycopterids by Gaudant (1968). Greenwood (1970) and Ma (1980, 1987) confirmed the presence of this structure in lycopterids. In the beginning, Ridewood suspected a possible homology between the hiodontid temporal fenestra and the clupeoid preepiotic fossa. Greenwood considered the temporal fenestra and the preepiotic fossa to be more analogous than homologous. I recently checked these two structures in lycopterids, hiodontids, and clupeoids, finding that both the temporal fenestra and the preepiotic fossa hold the same position and are bounded by the same bones (antero-dorsally by the parietal, ventrally by the pterotic, and posteriorly by the epiotic) in the skull of these fishes. Judging from the position and the elements taking part in the construction of the opening, I tentatively regard the temporal fenestra in hiodontids and lycopterids as the homologue of the preepiotic fossa in clupeomorphs (Grande, 1985b). A similar opening or fossa is also present in *Pantodon*, *Papyrocranus*, Osmeridae, and Salmonidae (pers. obs.). It is clear that such a widely distributed feature should not be used as evidence to support a special relationship between lycopterids and hiodontids (also see Chapter 5).

As regards the 84 characters used in my cladistic analysis, none can be defined as a unique synapomorphy (CI=1) shared by only lycopterids and hiodontids. This means a closest relationship between lycopterids and hiodontids is not supported.

Chang and Chou (1977) noted some of the plesiomorphic characters shared by lycopterids and all other osteoglossomorphs. They believed that lycopterids found in the Upper Jurassic-Lower Cretaceous freshwater deposits of eastern Asia are possible representatives of the early clade of Osteoglossomorpha, and they named the order †Lycopteriformes.

Although my study does not agree with Greenwood's (1970) "apomorph sister group" relationship between †Lycopteridae and Hiodontidae, a stem-group (see Wilson, 1992) (possible sister-group) relationship between †Lycopteriformes and all other osteoglossomorphs including hiodontids is supported because all of the lycopteriforms described thus far share at least four of the eight synapomorphies of Osteoglossomorpha discussed above: 15[1/2], number of epurals decreased to one or zero); 18[1], absence of supraorbital; 19[1], presence of primary bite of mouth between parasphenoid and basihyal; and 20 [1/2], 16 or fewer principal branched caudal fin rays (see Table 7-1A).

ii. Reconsideration of the Phylogeny of Hiodontiformes *sensu stricto*

The name Hiodontiformes was first coined by Taverne in 1979, when he included †Lycopteridae and Hiodontidae. Since the sister-group relationship between †Lycopteridae and Hiodontidae has been disproved, the placement of these two families in the same taxon should be discontinued. Hiodontiformes *sensu stricto* and Hiodontidae in this thesis are, thus, coextensive.

Previously, hiodontids were considered to be most closely related with notopterids and then placed in the same suborder Notopteroidei because they share a similar swim bladder-ear connection (e.g, Bridge, 1900; Regan, 1909; Berg, 1940; Greenwood, 1963, 1970; Greenwood et al., 1966; Cavender, 1966; Nelson, 1968; Patterson and Rosen, 1977; Grande, 1979; Lauder and Liem, 1983; Nelson, 1994). During my recent reexamination of the fossil and extant osteoglossomorphs from North America, I have made every effort to find even one unique character state to link hiodontids with notopterids, but failed. Chapter 5 discussed the absence of a special relationship between hiodontids and notopterids. The cladistic analysis of 84 charcters for this chapter (see Figs. 7-1 to 7-3) also supports the arguments stated in Chapter 5. When I include the three notopterid genera within the clade of Hiodontiformes *sensu stricto*, the tree length is greatly increased from 197 steps to 211 steps. This indicates that there is no close relationship between hiodontids and notopterids. In addition, the result of my analysis implies also the following conclusions.

1. Sister-group Relationship between Hiodontiformes *sensu stricto* and Osteoglossiformes– In comparison with †Lycopteriformes, Hiodontiformes *sensu stricto* share all the osteoglossomorph synapomorphies, of which 16[1] (absence of supramaxilla) and 24[1] (fusion of io4 with io5) are particularly important in linking Hiodontiformes with Osteoglossiformes.

As mentioned above, the absence of a supramaxilla seems to be a character state shared only by Hiodontiformes and Osteoglossiformes among the 40 taxa included in the cladistic analysis. Fishes in †Lycopteriformes have at least one supramaxilla. All the out-group taxa, except *Chanos*, have two supramaxilla. *Chanos* may have one supramaxilla (pers. obs.). Thus, the absence of a supramaxilla is here considered to be the most important synapomorphy linking Hiodontiformes *sensu stricto* to Osteoglossiformes.

The fused io4-5 (the upper posterior infraorbital) in osteoglossomorphs was previously considered to be homologous with io5 (e.g., Nelson, 1969b; Roellig, 1967; Kershaw, 1976; Taverne,1977, 1978) or io4 (e.g., Greenwood and Patterson, 1967). A comparison of this upper posterior infraorbital with the fourth and fifth infraorbitals in †*Leptolepis coryphaenoides* (see Arratia, 1994), †*Anaethalion* (Arratia, 1987), †*Cladocyclus* (Patterson and Rosen, 1977; Maisey, 1991), elopomorphs (Forey, 1973b), clupeomorphs (Grande, 1985b), and primitive euteleosts (see Patterson, 1970, and pers. obs.) suggests that this osteoglossomorph upper posterior infraorbital is most likely to be homologous with the fourth and fifth infraorbitals in those outgroup taxa. If so, a fused io4-5 could be another important synapomorphy to support the sister-group relationship between Hiodontiformes *sensu stricto* and Osteoglossiformes.

2. Monophyly of Hiodontiformes *sensu stricto*– As listed in Chapter 5, the diagnosis for Hiodontiformes *sensu stricto* is totally different from that defined by Taverne (1979: 109). Almost all the characters in Taverne's diagnosis are either plesiomorphies of teleosts or highly homoplastic. However, all species in the Hiodontiformes *sensu stricto* share the following synapomorphies that strongly support the monophyly of the order.

a. *17[1], seven-rayed pelvic fin.* In all teleosts, the number of pelvic fin rays exhibits three main states. State one, the pelvic fin consists of more than seven rays

(17[0]). This state is present in all the basal teleosts, such as †*Leptolepis*, †*Tharsis*, †*Anaethalion*, †*Allothrissops*, †*Cladocyclus*, in elopomorphs, and even in the primitive euteleosts (pers. obs.). State 2, pelvic fin contains only seven rays (17[1]). This state is seen only in the members of Hiodontiformes *sensu stricto*. State three, there are six or fewer pelvic fin rays (17[2]). This third state is commonly seen in †Lycopteriformes, Osteoglossiformes, and in clupeomorphs.

Chapter 6 discussed the phylogenetic significance of the number of the pelvic fin rays. The seven-rayed pelvic fin is considered to be an important character state defining the monophyly of the Hiodontiformes *sensu stricto* because of its fixed appearence in this fish group.

b. *23[1], opercle an irregular parallelogram.* Among the 40 taxa included in my study, the outline of the opercle shows five distinct states (Table 7-1B). State 1 (23[0]), opercle is more or less irregularly trapezoidal, usually with a round dorsal edge. Such an opercle is commonly seen in the basal teleosts, such as leptolepids (Nybelin, 1974), †*Anaethalion* (Arratia, 1987, 1994), ichthyodectiforms (Patterson and Rosen, 1977; Maisey, 1991), elopomorphs (Goody, 1969; Forey, 1973b), clupeomorphs (Grande, 1982a-b, 1985b), and lower euteleosts (Gregory, 1933, pers. obs.). The opercle in Mormyroidea is also somewhat irregularly trapezoidal in shape (see Taverne, 1968, 1972). State 2 (23[1]), opercle is an irregular parallelogram. All the members in Hiodontiformes *sensu stricto* have this type of opercle. State 3 (23[2]), opercle is oval or kidney-shaped. Fishes in †Lycopteriformes and Heterotidinae possess this type of opercle. State 4 (23[3]), opercle is subsemcircular in shape. This state is shared by †*Laeliichthys* and all members in Osteoglossinae. State five (23[4]), opercle is fan-shaped. Such an opercle is only seen in notopterids.

According to the distribution of the five opercular states on the shortest tree, an irregular parallelogram-shaped opercle is another synapomorphy of Hiodontiformes *sensu stricto*.

c. *35[1], dorsal arm of post-temporal more than twice as long as ventral arm.* This character state seems to be unique for hiodontiforms (pers. obs.). The dorsal arm of the post-temporal in lycopteriforms and all other studied taxa may be longer than the ventral arm, but never twice as long as the latter. In addition, the post-temporal shows the same proportions and same outline among all of the genera (including †*Yanbiania*) of Hiodontiformes *sensu stricto*.

d. *36[1/2], dorsal part of hyomandibular distinctly separate or double-headed and bridged.* The dorsal part of the hyomandibular articulating with

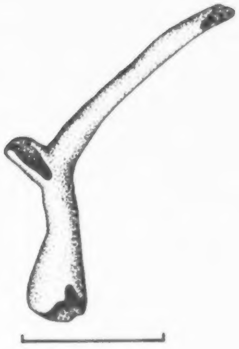


FIGURE 7-4: Triradiate dermosphenotic of *Hiodon alosoides*, drawn from UAMZ 6714. This type of dermosphenotic is uniquely present in all hiodontiforms. Scale bar equals 5mm.

the cranium has two basic states in the 40 taxa. It is single-headed in all the out-group taxa of Hiodontiformes *sensu stricto*, while in the ingroup taxa of this order, it is distinctly double-headed. My examination of this character discriminates two types of double-headed hyomandibular: a completely separated double-headed hyomandibular as seen in †*Eohiodon*, and a bridged double-headed hyomandibular seen in †*Yanbiania* and *Hiodon* (see Fig. 5-4). Nevertheless, a distinct double-headed hyomandibular appears to be another important synapomorphy of the Hiodontiformes *sensu stricto*.

e. *37[1], dermosphenotic triradiate.* My observations suggest that the dermosphenotic has two basic states in teleosts: it may be either (1) irregularly triangular or (2) triradiate. All teleosts except hiodontiforms included in my study share the first type of dermosphenotic (see Table 7-1B). Thus, a triradiate dermosphenotic (Fig. 7-4) is unique for Hiodontiformes *sensu stricto*.

iii. Synapomorphies of Osteoglossiformes

Since lycopterids and hiodontids are considered to belong to †Lycopteriformes and Hiodontiformes respectively, they have been removed from the Osteoglossiformes. The previous definition of Osteoglossiformes (see Nelson, 1994) needs to be narrowed or emended. This study suggests four synapomorphies for the Osteoglossiformes.

a. *7[2/3], uroneurals decreased to one or zero.* Except for †*Singida*, which has two uroneurals (see Greenwood and Patterson, 1967), †*Thaumaturus*, which also has two uroneurals (see Micklich, 1992), and †*Ostariostoma*, which has only one uroneural (see this chapter), all the members in Osteoglossiformes do not have any uroneurals in their caudal skeleton (pers. obs.). This situation was first noted by Whitehouse (1910) in *Notopterus*, and later by Greenwood (1966) in *Pantodon* and all osteoglossids. Since the states 7[2/3] are not present in any of the basal teleosts, elopomorphs, or clupeomorphs, and seldom seen in the relatively advanced teleosts examined in this study (see Table 7-1A), it is thought to be an important synapomorphy of the Osteoglossiformes.

b. *8[2/3], number of hypurals decreased to six or five.* The previous studies on both holostean (Nybelin, 1963, 1977; Patterson, 1973; Schultze and Arratia, 1986) and teleostean (including pholidophorid) caudal skeletons (see Gosline, 1960; Nybelin, 1963, 1971, 1973a-b, 1974; Greenwood, 1966; Patterson, 1968, 1970; Rosen, 1973; Eastman, 1980; Arratia, 1987, 1991; Arratia and Schultze, 1992; Schultze and Arratia, 1988, 1989) provide me with detailed information about the evolutionary trend of hypurals in teleosts. In the 40 taxa examined in this study, the state number of hypurals decreased to six or five occurs first in the Osteoglossiformes. A similar condition may be present in clupeomorphs and euteleosts, but it is possibly a convergence that will not affect the validity of 8[2/3] as one of the synapomorphies of the Osteoglossiformes.

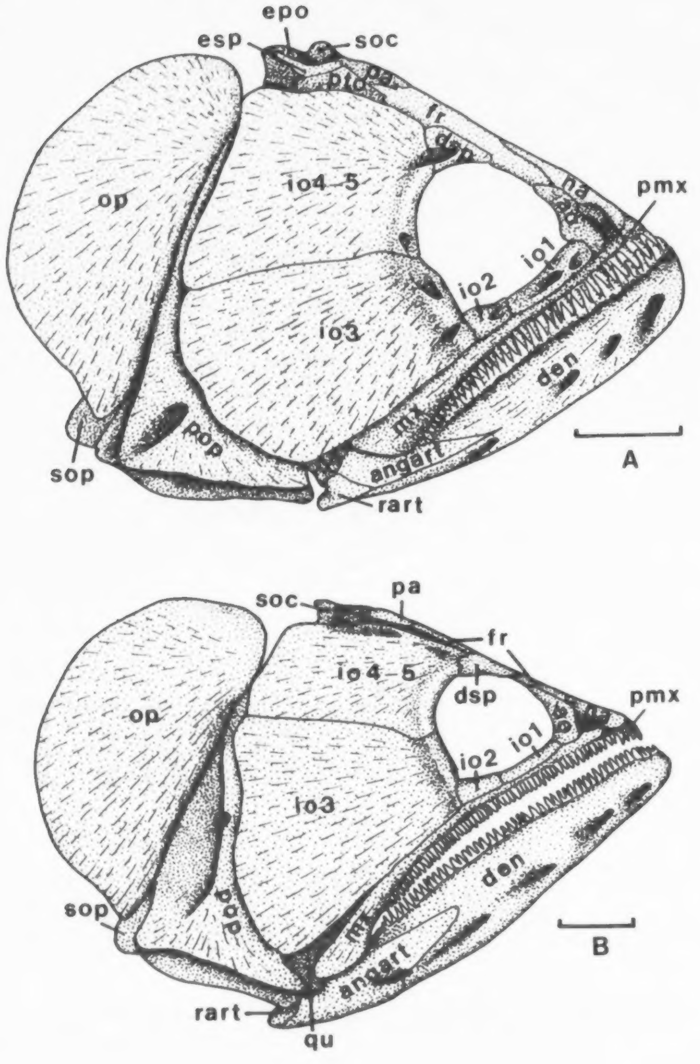
c. *20[2], 15 or fewer principal branched caudal fin rays.* As shown in Table 7-1A, all the members in the Osteoglossiformes, only with the exception of some mormyrids, have a caudal fin consisting of 15 or fewer principal branched rays. Species in the sister group Hiodontiformes have 16 principal branched caudal fin rays. In contrast, the caudal fin in all the basal teleosts and some of the primitive euteleosts consists of at least 17 branched principal rays.

d. *26[2], nasal gutter-like or irregularly subrectangular in shape.* My observations of the nasal in the 40 taxa suggests that the nasal has three basic states. State 1 (26[0]), nasal tubular but not curved. This is the situation seen in all the basal teleosts (see Nybelin, 1974, Patterson, 1967, Patterson and Rosen, 1977; Arratia, 1987), in elopomorphs (Forey, 1973b), clupeomorphs (Grande, 1985b), and in primitive euteleosts (see Patterson, 1970; Wilson and Williams, 1991; pers. obs.). State 2 (26[1]), nasal typically tubular and strongly curved. This second state of the nasal is present only in †*Hiodon consteniorum* sp. nov. and the two extant *Hiodon* species. State 3 (26[2]), nasal gutter-like and irregularly subrectangular. This state appears to be unique for all the taxa in the Osteoglossiformes and therefore is considered to be another important synapomorphy of the order.

iv. Remarks on Definitions of Osteoglossoidei and Notopteroidei

1. Three Important Diagnostic Features of Osteoglossoidei– As mentioned above, Osteoglossoidei used to contain Osteoglossidae, Pantodontidae, and †Singididae. My study suggests that there is not sufficient evidence to define Pantodontidae and †Singididae. Those characters thought to be diagnostic of Pantodontidae (Nelson, 1994) and †Singididae (Greenwood and Patterson, 1967) are mainly autapomorphies (or generic specializations) of *Pantodon* and †*Singida*. Since these two genera share all the character states that are considered to be synapomorphies of either Osteoglossidae or Osteoglossinae as well as one or more unique character states with the extant *Scleropages* and *Osteoglossum*, I have included them in the subfamily Osteoglossinae in this thesis. Thus, the Osteoglossoidei discussed here is coextensive with the Osteoglossidae. Osteologically, fishes in Osteoglossoidei share at least three synapomorphies.

a. *23[2/3], opercle oval or subsemicircular in shape.* Among the 40 taxa


epo
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pmx
io1
io2
io3
den
mx
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FIGURE 7-5: Cranial skeleton of the selected osteoglossids. **A**, *Scleropages* sp., modified from Kershaw (1976). **B**, *Osteoglossum bicirrhosum*, modified from Ridewood (1905). Scale bars for both **A** and **B** equal 10mm.

included in this study, a typical oval opercle (23[2]) is seen in Heterotidinae, while the opercle in all the members of Osteoglossinae is more or less subsemicircular (23[3]).

b. *29[1/2], first ural centrum bearing one or two fully developed neural spine(s).* Except in notopterids, all the out-group taxa bear no fully developed neural spine on the first ural centrum. In Osteoglossomorpha, a first ural centrum bearing one or two full neural spine(s) occurs first in the Osteoglossoidei. The similar situation seen in some notopterids is here considered to be possibly resulting from convergent evolution.

c. *33[1], pterygo-quadrate area behind and below orbit completely covered by infraorbitals.* This is a character state uniquely shared by all members in the suborder Osteoglossoidei (e.g., Fig. 7-5). In all of the out-group taxa, the pterygo-quadrate area behind and below the orbit is more or less exposed (pers. obs.).

These three character states are considered to be the most important for diagnosis of the Osteoglossoidei.

2. **Emended Diagnosis of Notopteroidei**– Because of the elimination of lycopterids and all hiodontids from this suborder, and also because of the combination of mormyroids with notopterids and ostariostomids in the same suborder, the content of the Notopteroidei of this thesis is totally different from that of any previously defined Notopteroidei. Correspondingly, the diagnosis for this suborder needs to be emended. The following five character states are thought to be the possible synapomorphies of the Notopteroidei.

a. *30[1], io2 more or less rectangular and moderate in size.* The second infraorbital has three basic states in teleosts. In most taxa, it is a small and slender bone (30[0]). Fishes in Heterotidinae have a large and irregularly trapezoidal io2 (30[2]). However, the io2 in all the notopteroids is subrectangular and moderate in size.

b. *51[1], shape of io3 irregularly rectangular.* As coded in Table 7-1C, the io3 also has three basic states in teleosts. Since a rectangular io3 is first seen in all notopteroids except *Notopterus* in the 40 taxa examined in this study, it is here considered to be an important diagnostic feature of Notopteroidei.

c. *52[1], presence of infraorbital ledge formed by lateral extension of orbital margin of io1 and io2.* This character state has never been mentioned before. My examinations indicate that all Notopteroidei, including †*Ostariostoma*, †*Thaumaturus*, and Mormyroidea, have a unique infraorbital ledge that is formed by the lateral extension of the orbital margin of io1 and io2 (Fig. 7-6).

d. *53[1], infraorbital canal on io1 to io3 open in a groove.* As shown in

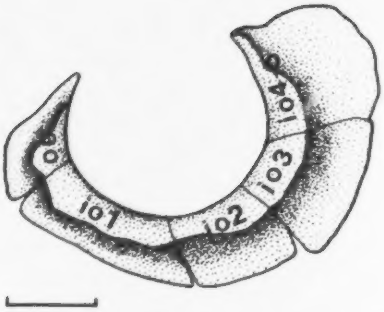


FIGURE 7-6: Infraorbital series of *Notopterus chitali* showing the infraorbital ledge and the open infraorbital canal on io1 to io3, based on UAMZ 6756. Scale bar equals 2mm.

Fig. 7-6, this character state seems to be first developed and shared by all the members referred to the Notopteroidei in this thesis. A similar condition (possible convergence) may be seen in euteleosts (Nelson, 1972a; pers. obs.), but it does not affect the validity of this character state as one of the synapomorphies of the Notopteroidei because it is not seen in any of the basal teleosts including elopomorphs.

e. *54[1], utriculus completely separated from sacculus and lagena.* According Lauder and Liem (1983: fig. 19, character 24), the utriculus in all notopterids and mormyroids is completely separated from the sacculus and lagena. Although I am not able to test this state in fossil taxa (e.g., †*Thaumaturus* and †*Ostariostoma*), this inner ear feature has so far not been reported in any other extant teleosts, and thus appears to be another unique synapomorphy of the extant Notopteroidei.

In conclusion, I adopt the hypothesis of the intragroup (interordinal) relationships of Osteoglossomorpha shown in Figs. 7-1 to 7-3. Although I have made a few essential alterations to the meaning of the Hiodontiformes *sensu stricto* and to the Osteoglossiformes, my study has resulted in sufficient evidence to support the monophyly of Osteoglossomorpha. This monophyletic supercohort is the sister-rgroup of the clade consisting of Clupeomorpha and Euteleostei. On the basis of the synapomorphies of the corresponding taxa discussed above, I propose the following higher-level classification and diagnoses of the Osteoglossomorpha.

Subdivision Teleostei

Superorder Osteoglossomorpha: teleosts differing from Clupeomorpha and Euteleostei in having the following features: number of epurals decreased to one or zero; supraorbital absent, supramaxilla absent (except for †Lycopteriformes); primary bite of mouth between parasphenoid and basihyal; 16 or fewer branched caudal fin rays; development of paired tendon bones on 2nd hypobranchial, intestine coiling to left of esophagus and stomach; and fusion of io4 with io5.

Order †Lycopteriformes: primitive osteoglossomorphs differing from Hiodontiformes and Osteoglossiformes in having: one supramaxilla; opercle kidney-shaped; io4 and io5 unfused (containing †Lycopteridae).

Order Hiodontiformes: osteoglossomorphs having: seven-rayed pelvic fin; irregular parallelogram-shaped opercle; dorsal arm of post-temporal more than twice as long as ventral arm; dorsal part of hyomandibular with two heads, bridged or unbridged; dermosphenotic triradiate (containing Hiodontidae).

Order Osteoglossiformes: osteoglossomorphs differing from †Lycopteriformes and Hiodontiformes in the following characters: uroneurals absent (if present, not more than two); number of hypurals decreased to six or five; 15 or fewer branched caudal fin rays; nasal gutter-like or irregularly subrectangular in shape.

Suborder Osteoglossoidei: osteoglossiforms in which: opercle is oval or subsemicircular in shape; first ural centrum bears one or two full developed neural spine(s); pterygo-quadrate area behind and below orbit is completely covered by infraorbitals (containing Osteoglossidae).

Suborder Notopteroidei: osteoglossiforms in which: io2 is more or less rectangular and moderate in size, io3 is irregular rectangular in shape; there is an infraorbital ledge formed by lateral extension of orbital margin of io1 and io2; infraorbital canal on io1 to io3 opens in a groove (exposed); utriculus is completely separated from sacculus and lagena (containing Notopteridae, Mormyroidea, †Ostariostomidae).

PHYLOGENY OF NORTH AMERICAN OSTEOGLOSSOMORPHS

Although I have synonymized †*Eohiodon falcatus* Grande with †*Eohiodon woodruffi* Wilson (see Chapter 5), my study of the new materials has resulted in adding two new genera and one new species to the record of North American fossil osteoglossomorph fishes (see Chapter 3-4, and 6). In total, 11 North American osteoglossomorph species are considered to be valid (Table 7-2); of these, five are in the Hiodontiformes, and six in the Osteoglossiformes. The following possible phylogenetic relationships are recognizable.

i. Sister-group Relationships in Hiodontiformes *sensu stricto*

1. †*Yanbiania* and †*Eohiodon* plus *Hiodon*– I (see Li, 1987) was confident when I recognized †*Yanbiania* as an early divergent group of Hiodontidae. This hypothesis is strongly supported by the five synapomorphies of Hiodontiformes discussed above.

2. †*Eohiodon* and *Hiodon*– Cavender (1966), Wilson (1974, 1977, 1978), and Grande (1979, 1984) all believed that the Eocene †*Eohiodon* is closely related with the extant *Hiodon*. My study confirms the sister-group relationship between †*Eohiodon* and

Hiodon, which is supported by at least two possible synapomorphies.

a. *25[1], ratio of length of frontal to length of parietal less than 2.* Among the previously named osteoglossomorphs, †*Eohiodon* and *Hiodon* are the first to have this derived character state (pers. obs.).

b. *56[1], sexually dimorphic anal fin.* This seems to be a unique character state shared by †*Eohiodon* and *Hiodon* because the anal fin in all the other taxa examined in this study does not show a sexual dimorphism like that seen in †*Eohiodon* and *Hiodon*.

Further investigation within the †*Eohiodon -Hiodon* clade recognizes three sister-species relationships.

2A. †*Eohiodon rosei* and †*Eohiodon woodruffi*– This sister-species relationship is suggested by 36[1], hyomandibular articulating with cranium by two distinctly separate heads that are equal in size.

2B. †*Hiodon consteniorum* sp. nov. and the Two Extant *Hiodon* species– †*Hiodon consteniorum* sp. nov. is the only known fossil species of *Hiodon*. The establishment of its closest relationship with the two extant species is based on five synapomorphies.

a. *26[1], nasal tubular and strongly curved.* As pointed out in the discussion of the synapomorphies of the Osteoglossiformes, my personal observation recognizes three basic states of the nasal in the 40 taxa, with the second state (nasal tubular and strongly curved) present only in †*Hiodon consteniorum* sp. nov. and the two extant *Hiodon* species. It is here considered to be phylogenetically important in linking the three *Hiodon* species in one clade.

b. *57[2], anterior portion of premaxilla lower than posterior portion.* This character state is unique for †*Hiodon consteniorum* sp. nov. and the two extant *Hiodon* species. The premaxilla in all the other taxa included in this study is anteriorly raised or higher than posteriorly.

c. *58[1], a postero-dorsal projection of opercle.* Since an opercle having a postero-dorsal projection is only seen in †*Hiodon consteniorum* sp. nov. and the two extant species, it is another unique character state shared by the species in *Hiodon*.

d. *59[1], a mid-dorsal concavity on premaxilla.* No one has previously reported this character state in teleosts. My study indicates that *Hiodon tergisus, H. alosoides*, and †*H. consteniorum* sp. nov. are the only three species sharing this state.

e. *61[1], neural spine on pu1 (npu1) rudimentary.* The neural spine on pu1 has three states. State 1, npu1 always completely developed. Most teleosts

TABLE 7-2: The revised North American fossil osteoglossomorph fishes.

DESCRIBED SPECIES	TIME NAMED	LOCATION	STRATIGRAPHIC DISTRIBUTION
†*Joffrichthys symmetroptera* gen. et sp. nov.	This Thesis	Red Deer	Paleocene, Paskapoo Formation
†*Cretophareodus alberticus* gen. et sp. nov.	This thesis	Near Wardlow	Middle Campanian, Oldman Formation
†*Phareodus encaustus*	(Cope) 1872	Fossil Lake	Eocene, Green River Formation
†*Phareodus testis*	(Cope) 1873	Fossil Lake	Eocene, Green River Formation
†*Eohiodon rosei*	(Hussakof) 1916	Kamloops	Eocene, Tranquille Beds
†*Eohiodon woodruffi*	Wilson 1978	Republic	Middle Eocene, Klondike Mountain Formation
†*Hiodon consteniorum* sp. nov.	This Thesis	Near Coal Creek	Late Eocene, Kishenehn Formation
†*Chandlerichthys strickeri*	Grande 1987	Arctic Slope	Albian or Cenomanian, Chandler Formation
†*Ostariostoma wilseyi*	Schaeffer 1949	Raw Liver Creek	Upper Cretaceous, Livingston Formation

including lycopteriforms and osteoglossiforms share this state. State 2, npu1 rudimentary when it is present. This state is uniquely seen in †*Hiodon consteniorum* sp. nov. and the two extant *Hiodon* species. State 3, npu1 absent in the caudal skeleton. This state is present in some euteleosts, such as osmerids and salmonids (pers. obs.).

2C. *Hiodon tergisus* and *Hiodon alosoides*– These two extant species share 60[1], presence of belly keel. Further investigation seems to be neccessary to find more significant character states to test this relationship since it is difficult to check this character state in fossil taxa.

ii. Sister-group Relationships in Osteoglossoidei Lineage

I adopt Nelson's (1994) classification of Osteoglossidae in which Heterotidinae and Osteoglossinae are included. The differences are (1) my Heterotidinae contains at least three fossil genera (†*Joffrichthys* gen. nov., †*Sinoglossus* Su 1986, and possibly the South American †*Laeliichthys* Santos, 1985), while Nelson's Heterotidinae contains only the two extant genera (*Heterotis* and *Arapaima*); and (2) besides †*Cretophareodus*, †*Phareodus*, and †*Brychaetus* (its validity is discussed below), I have also included *Pantodon* and †*Singida* in my Osteoglossinae, while Nelson included only the extant *Osteoglossum* and *Scleropages* in this subfamily.

In total, six North American fossil osteoglossiform species are recognized (see Table 7-2), five of them are referred to the family Osteoglossidae. The hypothetical phylogenetic relationships of the five North American fossil osteoglossid fishes may be reconstructed as follows.

1. †*Joffrichthys* and †*Sinoglossus-Heterotis-Arapaima* Clade– †*Joffrichthys* is a new genus named on the materials from the "fish-layer" at the Joffre Bridge road cut near Red Deer, Alberta. In Chapter 4, I have briefly discussed the taxonomic position of this new genus and the phylogeny of †*Sinoglossus*. The reasons that I place †*Joffrichthys* gen. nov. in the subfamily Heterotidinae are mainly the shape of the second infraorbital, the lengthened horizontal arm of the preopercle, the three branches of the preoperculo-mandibular canal on the horizontal arm of the preopercle, the anal fin as large as or slightly smaller than the posteriorly located dorsal fin, and the short distance between the small pelvic fin and the large anal fin. Of these features, the irregularly trapezoidal second infraorbital (30[2]) and the pattern of the preopercle (40[1]) are the most important character states linking †*Joffrichthys* gen. nov. with the Heterotidinae. Other preserved skeletal features of †*Joffrichthys* gen. nov. suggests that it is probably a sister-group of the clade consisting of the fossil †*Sinoglossus*, plus the extant *Heterotis* and *Arapaima*. This relationship is supported by two important character states.

a. *23[2], opercle oval in shape.* Although the opercle of †*Lycoptera* is also coded as 23[2], it is kidney-shaped but not oval. Only †*Joffrichthys*, †*Sinoglossus*, *Heterotis*, and *Arapaima* share a typical oval opercle among known osteoglossomorphs.

b. *63[1], posterior end of maxilla lying on dentary part of lower jaw.* This character has not been noted elsewhere. In all the out-group taxa, the posterior end of the maxilla lies on the angular portion of the lower jaw. †*Joffrichthys*, †*Sinoglossus*, *Heterotis*, and *Arapaima* are the only genera in which the posterior end of the maxilla lies on the dentary part of the lower jaw (Figs. 4-3, 4-4A, 4-6C, 4-9, and 4-10). I consider this character state to be the most important synapomorphy supporting the closest relationship between †*Joffrichthys* and the clade of †*Sinoglossus*, *Heterotis* plus *Arapaima*.

2. Possible Relationship between †*Chandlerichthys* and Heterotidinae– Since the the material (type specimen) used to establish the genus †*Chandlerichthys* is poorly preserved, Grande (1986) was uncertain of its systematic position in Osteoglossomorpha. I have made every effort to find more skeletal features to clarify this problem, but have not been very successful. Only 28 characters can be coded (see Table 7-1A-D). Of the 56 missing states for †*Chandlerichthys*, numbers 15[1/2], 19[1], 21[1], 22[1], and 24[1] are five of the eight synapomorphies of Osteoglossomorpha; also 7[3], 8[2/3], and 26[2] are three of the four important synapomorphies of Osteoglossiformes. Besides, all of the synapomorphies for Osteoglossoidei or Osteoglossidae (23[2/3], 29[1/2], 33[1]) and Heterotidinae (12[2], 30[2]) are unknown in †*Chandlerichthys*. Such a situation makes it impossible to carry out a satisfactory reconstruction of the phylogeny of this presumed osteoglossomorph fish from early Late Cretaceous fresh water deposits of North America.

However, Figs. 7-1 to 7-3 suggest an interesting relationship between †*Chandlerichthys* and †*Laeliichthys*. These two genera form a clade that is either the sister group of the subfamily Heterotidinae (Fig. 7-1), or the sister group of Osteoglossidae (Fig. 7-3), or lies in a polychotomy with Heterotidinae and Osteoglossinae (Fig. 7-2). The relationship between †*Chandlerichthys* and †*Laeliichthys* is supported only by 66[1], the angle formed by the vertical and horizontal arms of the preopercle being less than 90°. However, †*Chandlerichthys* and †*Laeliichthys* are the only two genera included in this study that have a preopercular angle less than 90°. These two genera might represent an earlier radiation of Heterotidinae. Any attempt to clarifiy this issue seems unlikely to succeed unless sufficient new material of

†*Chandlerichthys* can be found in the future.

3. †*Cretophareodus* gen. nov. and the †*Phareodus* -†*Brychaetus* Clade– †*Cretophareodus* gen. nov. is the sister group of the clade consisting of †*Phareodus* and †*Brychaetus* (Chapter 3) when the data matrix for cladistic analysis contains only 12 taxa (Fig. 3-5). In this chapter, the position of †*Cretophareodus* gen. nov. varies according to two topologies when 40 taxa are included in the cladistic analysis. In the two consensus trees produced by PAUP 3.1.1 (Figs. 7-2 and 7-3), it lies in a polychotomy with the †*Phareodus* clade, *Pantodon*, †*Singida*, and the clade consisting of *Osteoglossum* and *Scleropages*. In the shortest tree preferred here (Fig. 7-1), this new genus takes the same position as that shown in Fig. 3-5. This phylogenetic relationship is supported by at least one synapomorphy, 46[1]: the frontal is anteriorly greatly expanded laterally to form an anterior portion at least 1.5 times as broad as the posterior portion of the bone. This character state is not present in any of the other teleosts included in this study. It is, therefore, considered to be of phylogenetic significance. A more detailed discussion of the relationship between †*Cretophareodus* and the clade of †*Phareodus* -†*Brychaetus* is given in Chapter 3.

4. Remarks on the Relationship between †*Phareodus* and †*Brychaetus*– Figs. 7-1 to 7-3 show an unexpected topology suggesting that †*Brychaetus muelleri* is more closely related to †*Phareodus encaustus* and †*P. queenslandicus* than †*Phareodus testis* is to these two species. This suggests either that †*Phareodus* (Leidy, 1873) is a paraphyletic group or that †*Brychaetus* is a synonym of †*Phareodus* (Figs. 7-1 to 7-3).

†*Brychaetus* was named based only on the cranial skeleton. The original diagnosis for this genus (Woodward, 1901) is thus not complete. Fortunately, Roellig (1967, 1974) and Taverne (1974, 1978) late made a detailed investigation of the material referred to †*Brychaetus*. From the description given by Roellig and Taverne, I found that it is difficult to distinguish †*Brychaetus* from †*Phareodus* in known cranial skeletal characters. The following three character states shared only by †*Brychaetus muelleri*, †*Phareodus testis*, †*P. encaustus*, and †*P. queenslandicus* strongly suggest that †*Brychaetus* is included in the same clade as †*Phareodus*.

a. *46 [2], anterior portion of frontal at least twice as broad as posterior portion.* This state is probably derived from 46[1], which is the most important synapomorphy linking †*Cretophareodus* with the clade of †*Phareodus* plus †*Brychaetus* in Fig. 7-1. A frontal with an anterior portion at least twice as broad as the posterior portion is not present in any of the outgroup taxa. Such a frontal is considered to be a unique character state supporting the closest relationship between †*Brychaetus* and †*Phareodus.*

b. *47[1], ratio of depth to width of opercle greater than 2.* According to Patterson (1967), Nybelin (1974), Patterson and Rosen (1977), Arratia (1987, 1994), and Maisey (1991), the opercles in basal teleosts may be either slightly deeper than broad or broader than deep. None of them has a depth twice the width. A similar condition is also commonly seen in Elopomorpha (Forey, 1973b), Clupeomorpha (Grande, 1985b), and Euteleostei (Gregory, 1933, Patterson, 1970). In Osteoglossomorpha, the ratio of depth to width of the opercle may reach to 1.5, or greater than 1.5 in some genera, such as *Osteoglossum* and *Scleropages,* but never exceed 2 (pers. obs.). Therefore, †*Phareodus* and *Brychaetus* are the only two members in Osteoglossomorpha sharing an opercle that has a ratio of depth to width greater than 2.

c. *48[1], extrascapular (supratemporal) slender and distinctly angular.* According to my observations, the extrascapular in most teleosts (when it is present) may be either somewhat triangular (e.g. that in †*Allothrissops, Hiodon*, and most clupeomorphs) or subtrapezoidal or squarish (e.g. that in some euteleosts). A slender and distinctly angular extrascapular (see Figs. 2-2A, 2-3, 2-8B, and 2-9) is seen only in †*Phareodus* and †*Brychaetus.* It is here considered to be of great phylogenetic significance.

What follows are reconstructions of the hypothetical phylogenetic relationships among the four species of †*Phareodus* and †*Brychaetus.*

4A. Sister clade of †*Phareodus testis*– Since †*Phareodus testis* shares only 46[2], 47[1], and 48[1] (see the above discussion), it is, thus, equally closely related to †*Brychaetus muellerii*, †*P. encaustus*, and †*P. queenslandicus.* In contrast, †*Brychaetus muellerii* appears to have a more intimate relationship with †*P. encaustus* and †*P. queenslandicus* because it shares at least the following two unique character states with those two species.

a. *49[1], preopercle curved with no distinct horizontal arm.* Only †*Brychaetus muellerii,* †*P. encaustus*, and †*P. queenslandicus* have this type of preopercle among studied taxa. The preopercle in all the other teleosts is angular with a distinct horizontal arm.

b. *50[1], hyomandibular with a greatly expanded subtriangular anterior wing.* A normal outline of the anterior part of the hyomandubular does not include an anterior expansion. †*Brychaetus muelleri* seems to be the only species sharing this character state with †*P. encaustus* and †*P. queenslandicus.*

These two character states strongly suggest that †*Brychaetus* is synonymous with

†*Phareodus*, it is, thus, a junior synonym of the latter. This verification (also see Chapter 2) results in an emended †*Phareodus* that contains four species (see Figs. 7-1 to 7-3).

4B. Two most Closely Related Species in †*Phareodus*– Unlike some previous assertions (see Taverne, 1973, 1979; Grande, 1984), my study suggests that †*Phareodus encaustus* and †*Phareodus queenslandicus* are the two most closely related species in the emended genus †*Phareodus*. This close relationship is supported by 51[2], the lower infraorbital behind the orbit (io3) long and shallow. In contrast, in all other teleosts, io3 is either short and deep (e.g. that in †*Ascalabos voithii* and †*Leptolepis coryphaenoides*, see Arratia, 1994; *Osteoglossum* and *Scleropages*, see Fig. 7-5) or irregular rectangular (e.g. that in all notopteroids, Ridewood, 1904; Taverne, 1968, 1972, 1978; and pers. obs., and that in osmerids, Wilson and Williams, 1991, and pers. obs.). According to Taverne (1974, 1978), an elongate and shallow io3 appears also to be present in †*P.* (†*Brychaetus*) *muellerii* (Woodward). I am doubtful of this because there are many discrepancies among the restorations given by Roellig (1974) and Taverne (1974), and Woodward's (1901) original illustrations for that structure.

iii. Reassessment of the Phylogeny of †*Ostariostoma*

†*Ostariostoma* Schaeffer 1949 is a genus named on the basis of only one specimen (PU14728, originally in Princeton University collection, now deposited at Peabody Museum of Natural History, Yale University). Although Schaeffer (1949) provisionally assigned this genus to the suborder Clupeoidei (Schaeffer's spelling was Clupeoidea), he mentioned another possible relationship between †*Ostariostoma* and the ancestral lineage of Ostariophysi. Grande and Cavender (1991) admitted that †*Ostariostoma* is a perplexing fish in terms of its relationships when they redescribed this genus. They thought that the problems were arise mainly from both the insufficient preservation and the features preserved on the specimen. On the one hand, Grande and Cavender ruled out the posibilities that †*Ostariostoma* could be an ostariophysan (because there is no modification of anterior vertebral elements), an elopomorph (because there are no rostral or prenasal ossicles), or a clupeomorph (because there are no scutes, no recessus lateralis, and no clupeomorph-type caudal skeleton). On the other hand, they pointed out two other possibilities, that it might be either an osteoglossomorph or a primitive non-ostariophysan euteleost. Tentatively, Grande and Cavender believed that †*Ostariostoma* appears to be most closely related with Osteoglossomorpha (perhaps a hiodontoid) based on the presence of 18 principal caudal fin rays, the absence of a supramaxilla, and the

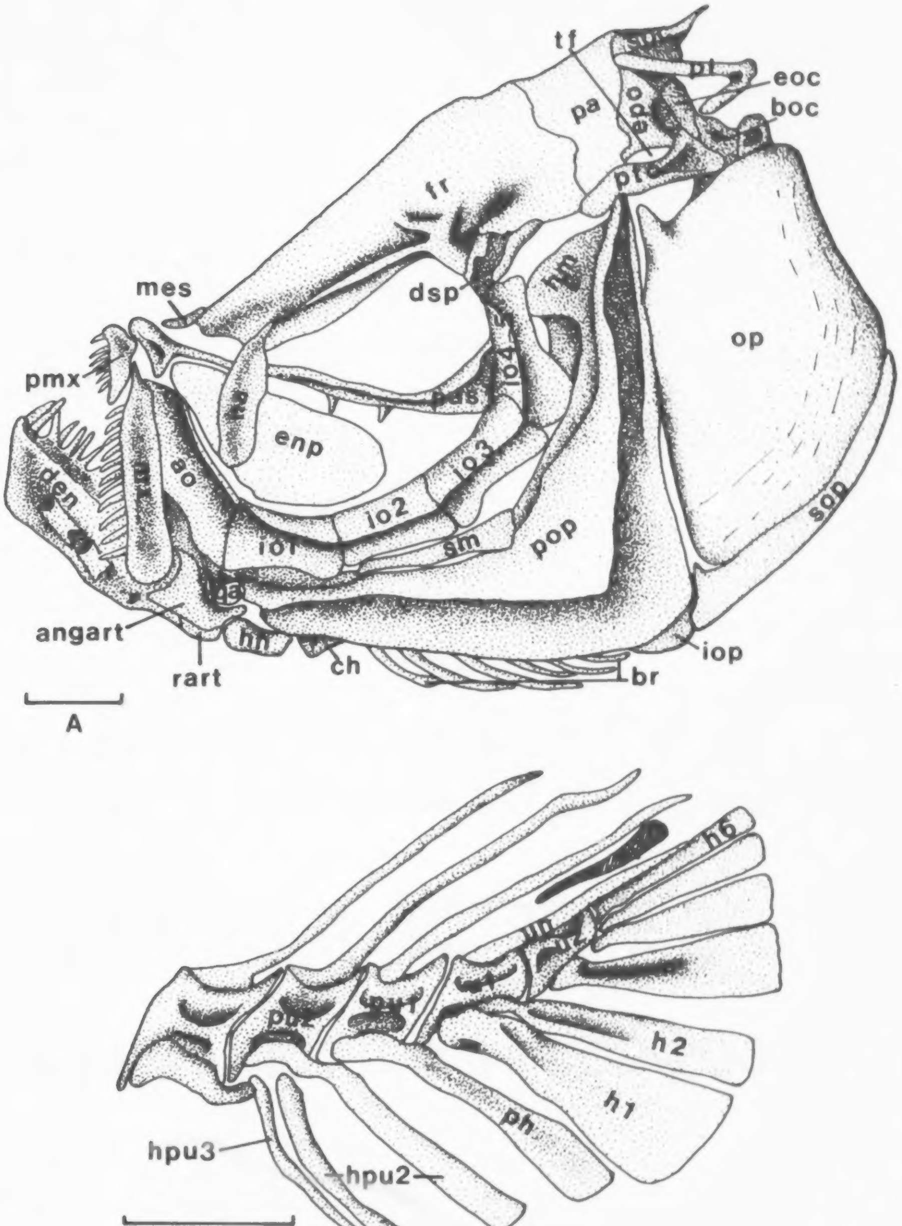
possible presence of a hiodontid-like anal fin.

My study of both the holotype and its cast suggests that it is unlikely that †*Ostariostoma* is a hiodontiform fish because it does not possess 17[1] (seven-rayed pelvic fin, *versus* four-rayed in †*Ostariostoma*), 23[1] (opercle irregularly parallelogram-like, *versus* irregularly trapezoidal in †*Ostariostoma*), 35[1] (dorsal arm of post-temporal more than twice as long as ventral arm, *versus* less than twice in †*Ostariostoma*), 36[1/2] (dorsal part of hyomandibular distinctly with two separate or bridged heads, *versus* a single head in †*Ostariostoma*), and 37[1] (dermosphenotic triradiate, *versus* somewhat square in †*Ostariostoma*).

It is notable that most of my observations on the specimen of †*Ostariostoma* (see Figs. 7-7) agree with Grande and Cavender's description. The only disagreements are: (1) the antorbital (ao) designated by Grande and Cavender is here considered to be the displaced nasal based on its gutter-like shape and its strongly curved posterior end; (2) the possible nasal (na?) designated by Grande and Cavender is thought to be the mesethmoid; (3) the large bone labeled as a lacrimal (l) by Grande and Cavender includes two bones, the lacrimal (the first infraorbital) and the second infrorbital; (4) the second infraorbital (io2) recognized by Grande and Cavender is the 3rd infraorbital; (5) the temporal fenestra (tf) is considered to be the homologue of the preepiotic fossa; (6) the epural (epu) designated by Grande and Cavender is thought to be the distal part of the broken neural spine of the first preural; (7) the bone labeled by "?" in Grande and Cavender's paper is here thought to be the epural; and (8) I believe that this fish has only one uroneural in its caudal skeleton.

The cladistic analysis of 84 characters and their states in 40 taxa yields a new picture of the phylogeny of †*Ostariostoma* in Osteglossomorpha (see Figs. 7-1 to 7-3). This new picture suggests that †*Ostariostoma* is an osteoglossiform because it shares at least 7[2] (uroneurals decreased to one), 8[2/3] (number of hypurals decreased to six or five), 20[2] (15 or fewer principal branched caudal fin rays), and 26[2] (nasal gutter-like) with all the other members in the Osteoglossiformes. When I move this genus from the clade of Osteoglossiformes to the clade of Hiodontiformes, the tree length is increased from 197 steps to 209 steps. This is evidently not the best choice.

In the clade of Osteoglossiformes, †*Ostariostoma* is linked with all other notopteroids including †*Thaumaturus*, based on the data in Gaudant (1981, 1988) and Micklich (1992), by 30[1] (io2 more or less rectangular and moderate in size), 51[1] (io3 an irregular rectangle), 52[1] (presence of infraorbital ledge), and 53[1] (infraorbital canal on io1 to io3 open in a groove).


tf
soc
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enp
io3
den
mx
ao
io2
io1
sm
pop
sop
qa
angart
hh
ch
iop
rart
br
A
h6
un
pu2
pu1
h2
h1
ph
hpu3
hpu2
B

FIGURE 7-7: Revised restoration of the cranial (**A**) and caudal (**B**) skeleton of †*Ostariostoma wilseyi*, drawn from the cast of PU 14728. Scale bars for both **A** and **B** equal 1mm.

Further investigation indicates that †*Ostariostoma* forms a clade with †*Thaumaturus,* which is defined by three homoplasies (7[2], single uroneural; 55[1], strongly upturned mouth cleft; and 73[1], preoperculo-mandibular canal on vertical arm of preopercle open in a groove). This clade is most closely related to Mormyroidea by two homoplasies (40[1], length of vertical arm of preopercle about as long as horizontal arm; and 42[1], basihyal tooth plate fused with basibranchial tooth plate).

In conclusion, fossil osteoglossomorphs from North America are closely related with the extant taxa of all of the main groups such as Hiodontidae, Heterotidinae, Osteoglossinae, and Mormyroidea or Notopteroidei (Fig. 7-8). They thus provide important linkages for further discussion of the early derivation and evolution of Osteoglossomorpha.

IV. COMMENTS ON HISTORICAL BIOGEOGRAPHY OF OSTEOGLOSSOMORPHA

In comparison with many other teleostean groups, the monophyly of Osteoglossomorpha is relatively well established (see the above discussion). This group also has a relatively well-preserved fossil record from Late Jurassic to Oligocene deposits of the world (Fig. 7-8), nearly all representing undoubted freshwater habitats. This record provides data for investigation of the historical biogeography of Osteoglossomorpha, which is particularly significant to the study of the history of the freshwater fish faunas in the world.

i. Previous Work on Osteoglossomorph Historical Biogeography

Since Nelson (1969b) first applied the cladistic dispersal method (Patterson, 1981a) to the analysis of osteoglossomorph biogeography, the subject has evoked a series of discussions on the origin of the Recent distribution of Osteoglossomorpha. Nelson, based on his study of infraorbitals, believed that Africa could be the center of the ancestral distribution of osteoglossomorphs; accordingly, the presence of Hiodontidae in North America could be secondary and of relatively late occurrence. Greenwood (1970) and Zhang and Zhou (1976), upon the establishment of the relationship between †*Lycoptera* and Hiodontidae, suggested that osteoglossomorphs might have been distributed ancestrally in East Asia, later reaching North America and southern continents. Patterson (1975, 1981b) raised the possibility of marine dispersal of the

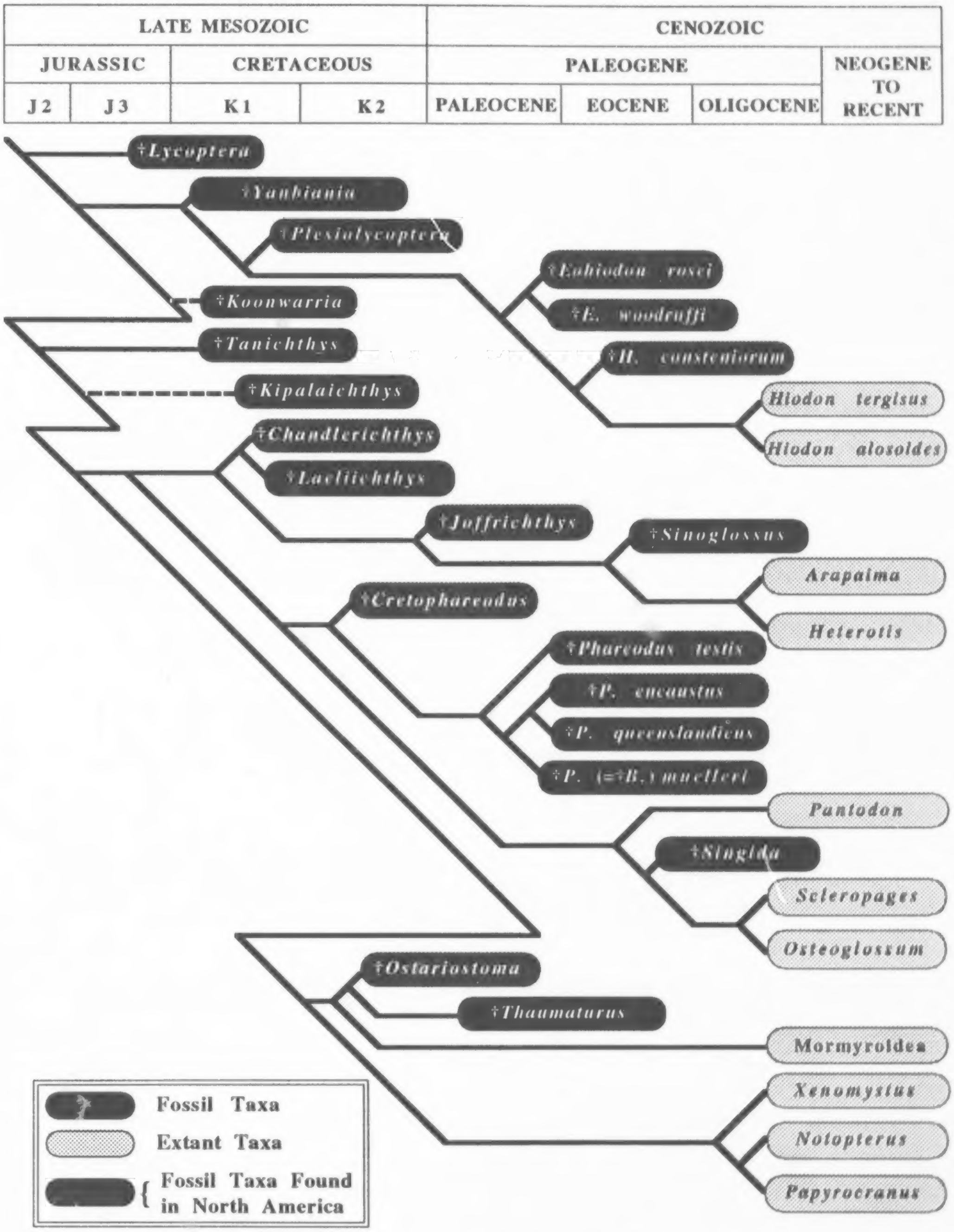
LATE MESOZOIC
CENOZOIC
JURASSIC
CRETACEOUS
PALEOGENE
NEOGENE TO RECENT
J2
J3
K1
K2
PALEOCENE
EOCENE
OLIGOCENE
†Lycoptera
†Yanbiania
†Plesiolycoptera
†Koonwarria
†Tanichthys
†Kipalaichthys
†Eohiodon rosei
†E. woodruffi
†H. consteniorum
Hiodon tergisus
Hiodon alosoides
†Chandlerichthys
†Laeliichthys
†Joffrichthys
†Sinoglossus
Arapaima
Heterotis
†Cretophareodus
†Phareodus testis
†P. encaustus
†P. queenslandicus
†P. (=†B.) muelleri
Pantodon
†Singida
Scleropages
Osteoglossum
†Ostariostoma
†Thaumaturus
Mormyroidea
Xenomystus
Notopterus
Papyrocranus
Fossil Taxa
Extant Taxa
Fossil Taxa Found in North America

FIGURE 7-8: Diagram showing the hypothetical evolutionary history of Osteoglossomorpha. Note that all the main lineages of this fish group had a North American distribution. †*E.*, †*Eohiodon*; †*H.*, †*Hiodon*; †*P.*, †*Phareodus*; †*B.*, *Brychaetus*.

ancestral lineage of Osteoglossoidei based on the discovery of †*Brychaetus* in marine deposits. I (Li, 1987) further discussed the historical biogeography of Hiodontidae based on recognition of a later Early Cretaceous hiodontid †*Yanbiania*, believing that Hiodontidae were originally distributed in northeastern Asia. All these hypotheses considered dispersal to be the major factor affecting osteoglossomorph biogeography.

Recently, the cladistic vicariance approach (Platnick and Nelson, 1978; Rosen, 1975, 1978, Nelson and Platnick, 1980, 1981; Grande, 1985a; Wiley, 1988; Brooks, 1990) has been applied to the transoceanic relationships of Osteoglossomorpha. Gayet (1987) believed that the present distribution of osteoglossomorphs could be the result of the fragmentation of a hypothetical "lost Pacifica" (Nur and Ben-Avraham, 1981). A similar idea was also held by Shen (1989), who suggested that an "ancestral land block," partly consisting of East Asia, North America, and Gondwana, might have been present.

Attempts to explain the trans-Pacific relationships of North American fossil and Recent osteoglossomorphs have also been made by Grande (1985a, 1989), who proposed a general biological pattern involving the early Tertiary of western North America; and by Wilson and Williams (1993), who suggested that the present endemic distribution of hiodontids may be a remnant of a former widespread northern-hemispheric distribution.

It is now evident that the historical biogeography of Osteoglossomorpha is much more complicated than what has been discussed or expected. Biogeographers or ichthyologists could be misled if they rely only on one model while neglecting the other; as well, they may be misled even if they have considered both the dispersal and the vicariance model but ignore the fossil evidence. Grande (1985a), Bänärescu (1990), Wilson and Williams (1993, partly), for example, recently summrized the argumentation between dispersal and vicariance models. It seems to me that the main contradictions between these two models are: 1) dispersal looks upon the sequence of fossil records and consents to use fossil as evidence in reconstructing the historical biogeography of a taxon, while vicariance emphasizes the incompleteness of fossil records and therefore refrains from considering the use of fossil evidence; 2) dispersal explanations assume that enlargement and shifting of the distribution area of a taxon is common and require the presence of an ancestral distribution area (centre of origin); while vicariance explanations assume that fragmentation of whole biotas is common and ignore the centres of origin. A critical survey of the principles of both dispersal and vicariance models affirms the rationalities of these two models. Either dispersal or vicariance is unlikely without movement. The only difference is that the dispersal model emphasizes the movement of a lineage from one area to another (actively or passively), while the

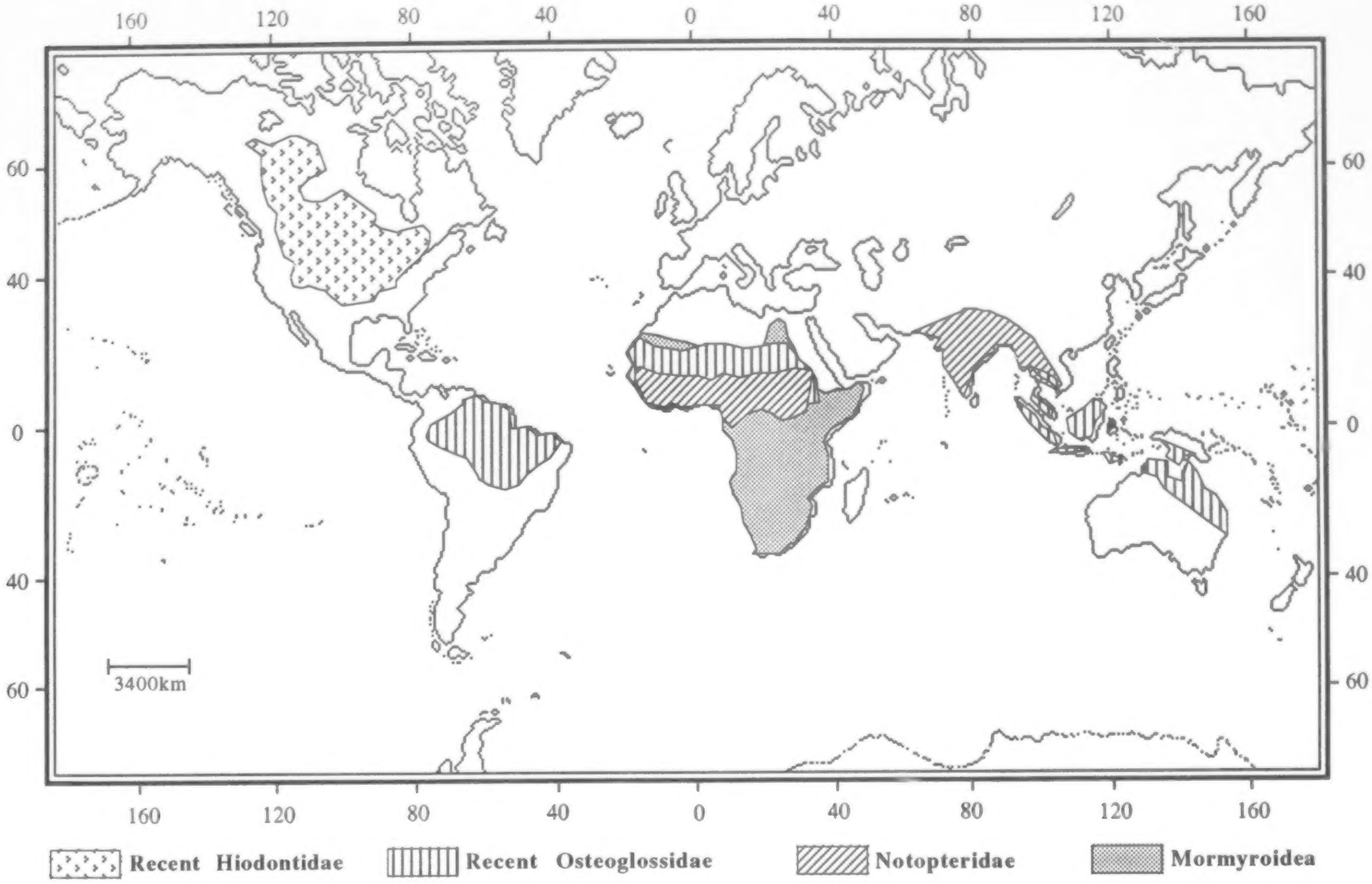
160
120
80
40
0
40
80
120
160
60
40
0
40
60
3400km
Recent Hiodontidae
Recent Osteoglossidae
Notopteridae
Mormyroidea

FIGURE 7-9: Map showing the modern geographic distribution of Osteoglossomorpha.

vicariance model stresses the subdivision and possible movement (drift) of the land mass carrying that lineage. In practice, these two processes might both have alternatively functioned during the biogeographical history of a lineage.

As regards the fossil evidence, I agree with Grande (1985a) in basic conceptions. There are at least four basic functions of fossil evidence: (1) providing additional taxa data in addition to those provided by Recent species, (2) providing additional taxa that increase the known biogeographic range of a lineage, (3) establishing a minimum age of a taxon, and (4) demonstrating area relationships that are not recognizable from later fossil or from extant biotas.

I believe both cladistic vicariance and dispersal events might have contributed to the establishment of the Recent distribution of Osteoglossomorpha. The known fossil records of this group, from the Upper Jurassic to the Oligocene and from all the continents except Antarctica provide this study with the general key of "time-control" (Grande, 1985a).

ii. Other Possible Interpretations of Osteoglossomorph Historical Biogeography

A great deal of effort has been made to propose a parsimonious hypothesis explaining the transoceanic relationships of Osteoglossomorpha. Fig. 7-8 briefly summarizes the evolutionary history (vertical distributions) of Osteoglossomorpha, and Figs. 7-9, 7-10, and 7-11 were derived from this by plotting the taxa known from different periods on maps. All these illustrations provide a framework for discussion of the following hypotheses.

1. Early Development of Osteoglossomorpha Occurred in Pangaea – As shown in Fig. 7-10, the known earliest record of Osteoglossomorpha is the Late Jurassic or Early Cretaceous †*Lycoptera*. In addition, fossil teleosts considered to be the ancestral lineages of Osteoglossomorpha have been reported from the Lower Cretaceous of the northeastern part (†*Yanbiania*) and the central and southern parts of East Asia (e.g., †*Tanichthys* Jin, 1991; †*Paralycoptera* Chang and Chou, 1977), from the Albian to Cenomanian (†*Chandlerichthys*) and Campanian to Maastrichtian (†*Cretophareodus* gen. nov. and †*Ostariostoma*) of North America, the Aptian of South America (†*Laeliichthys*), the Cenomanian of Africa (†*Kipalaichthys*, see Taverne, 1979), and possibly from the Lower Cretaceous of Australia (†*Koonwarria* Waldman, 1971). Judging from the preserved skeletal characters, these genera seem unlikely to be the earliest lineages of Osteoglossomorpha because they already share most of the osteoglossomorph synapomorphies with their extant relatives (see Fig. 7-1 and Table

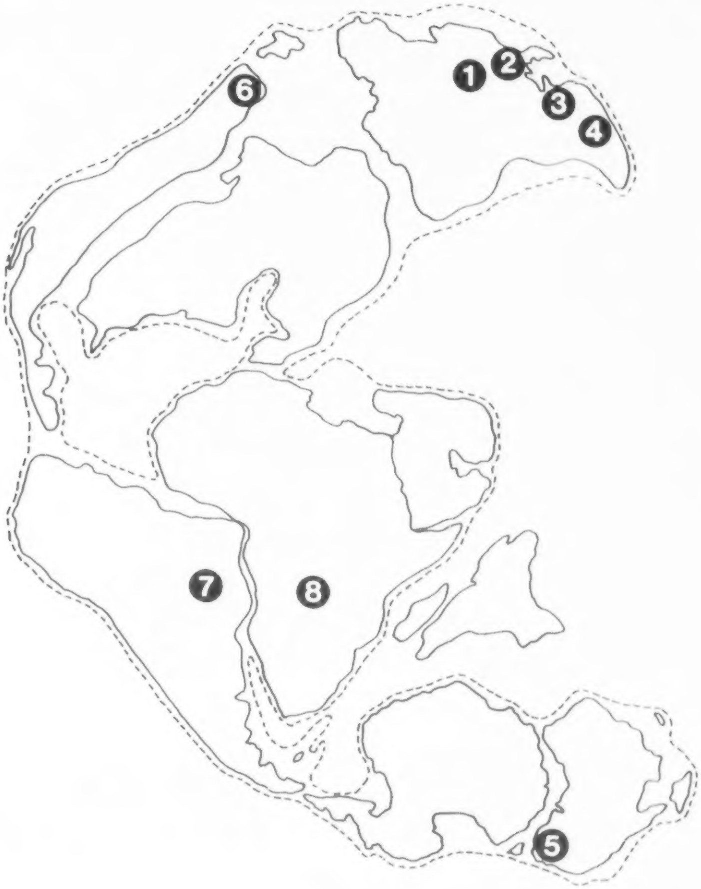

FIGURE 7-10: Sketch map showing fossil evidence for the Early Cretaceous to early Late Cretaceous distribution of Osteoglossomorpha. **1** †*Lycoptera*, **2** †*Yanbiania*, **3** †*Tanichthys*, **4** †*Paralycoptera*, **5** †*Koonwarria*, **6** †*Chandlerichthys*, **7** †*Laeliichthys*, and **8** †*Kipalaichthys*.

7-1A-D). Some of them (e.g., †*Yanbiania*) are distinguished from their extant relatives only by relatively minor features. As regards the distributions of these genera, they occupied most of the main land masses of the splitting Laurasia and Gondwana. It seems very difficult to interpret these data by suggesting the early development of Osteoglossomorpha in "Africa"(Nelson, 1969b) or in "East Asia" (Greenwood, 1970; Chang and Chou, 1977). These two hypotheses demand that the ancestors of Osteoglossomorpha would have to make at least four transoceanic dispersals from Africa to South America, North America, Australia, and East Asia; or, from East Asia to North America, Australia, South America, and Africa during the time between the Late Jurassic and the Late Cretaceous. The idealized hypothesis of a "lost Pacifica" (Gayet, 1987) is even more unparsimonious than the suggestions of "African origin" or "Asian origin" because it needs at least two vicariance events and drifts in three directions followed by collisions of the fragments of the so-called "lost Pacifica" with East Asia, North America, and South America, and at least one transoceanic dispersal from South America to Africa during the same time. Besides, there is no geological evidence for such a continent.

The ancestors of Osteoglossomorpha were most likely more plesiomorphic than †*Lycoptera*, †*Yanbiania*, †*Chandlerichthys*, †*Koonwarria*, †*Laeliichthys*, and *Kipalachthys*. They could have well existed much earlier and had a much more widespread distribution than any of these Late Jurassic or Early Cretaceous genera.

According to current ideas about plate tectonics, the most likely ancient landmass available as an ancestral distribution area of Osteoglossomorpha is Pangaea, a supercontinent thought to be present from the end of the Permian to the Late Jurassic. It seems probable that the early development of Osteoglossomorpha was accomplished in Pangaea by the time of the Middle to the Late Jurassic, and that the earliest of the main lineages of this group had already enlarged their distribution to most parts of Pangaea before its final splitting (Fig. 7-10). It seems to me that this is the most parsimonious suggestion in comparison with the hypotheses of "lost Pacifica," the "African origin," or the "East Asian origin," being subject to extinction of representatives from many continents (see Fig. 7-9). Fossil evidence documenting this hypothesis comes from India (Hora, 1938) and all the main continents except Antarctica (Figs. 7-10 and 7-11).

2. Lycopteriformes are a Stem Group of Osteoglossomorpha Endemic to East Asia– In terms of the available earliest fossil record of †*Lycoptera*, the ancestral lineage of †Lycopteriformes probably entered East Asia before the Late Jurassic, inhabiting the freshwaters of North China, Mongolia, and eastern Siberia (east of Baikal Lake), an area

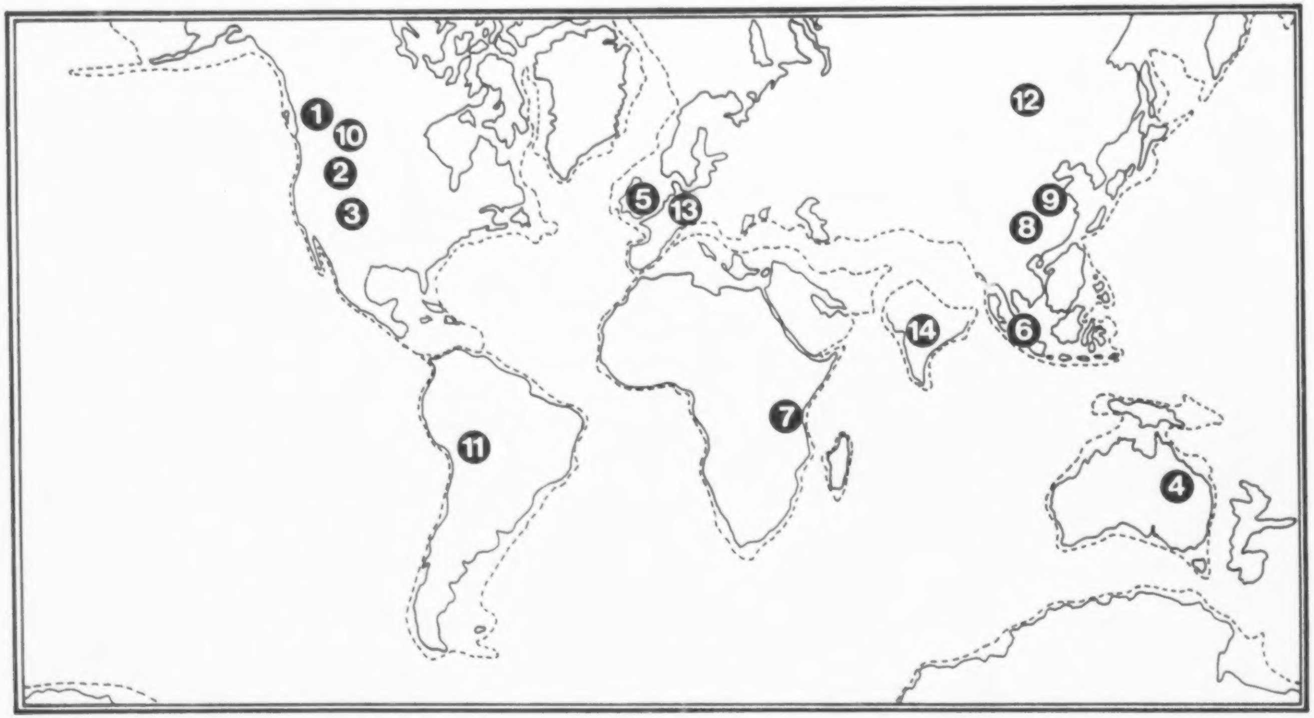

FIGURE 7-11: Sketch map showing the Early Tertiary distribution of Osteoglossomorpha. **1** †*Eohiodon*, **2** †*Ostariostoma*, †*Hiodon consteniorum*, **3** †*Phareodus*, †*Eohiodon*, **4** †*Phareodus queenslandicus*, **5** †*Phareodus* (=† *Brychaetus*) *muelleri*, **6**†*Musperia*, **7** †*Singida*, **8** †*Sinoglossus*, **9** ?† *Phareodus* sp., **10** †*Joffrichthys*, **11** †*Phareodusichthys* (Gayet, 1991), **12** †*Plesiolycoptera* († *Gobihiodon*) *parvus* (Sytchevskaya, 1986), **13** †*Thaumaturus*, **14** fossil scales of Osteoglossiformes.

ranging from 35°-60°N and 95°-135°E (Li, 1987). This distribution of †Lycopteriformes (†*Lycoptera* and †*Tongxinichthys* Ma, 1980) lasted from at least the Late Jurassic to the Early Cretaceous. As far as I know, there is no certain report of Lycopteriformes outside of East Asia. This situation may be simply asserted as owing to the incompleteness of the fossil record or extinctions of lycopteriforms from North America, South America, Europe, India, Africa, Australia, and Antarctica.

However, evidence from geological investigation indicates another possibility: that †Lycopteriformes is a lineage endemic only to East Asia. During the Late Jurassic to Early Cretaceous time, East Asia was separated from Euramerica by the epicontinental Turgai Sea, and from all the southern continents by the eastern part of the Tethys Sea (see Smith and Briden, 1977, Smith et al., 1981; Olsen, 1979; Pielou, 1979; Briggs, 1986). In addition, there was no connection between western North America and East Asia at that time. These divisions might have functioned as barriers that prevented †Lycopteriformes from being distributed over North America, Europe, and all the southern continents, and therefore, limited the enlargement of the distribution area of this early lineage of Osteoglossomorpha. Thus, it is reasonable to suggest, at present, that †Lycopteriformes is a lineage endemic only to East Asia, and to predict that its fossils will never be found outside of that area.

3. Some Difficult Problems– In conclusion, the historical biogeography of Osteoglossomorpha is an interesting topic, but it is very difficult to interpret. There are at least following perplexing questions that remain for students working on Osteoglossomorpha.

1) Fossil hiodontiforms have been known from East Asia and North America, while the extant hiodontiforms are seen only in North America. In contrast, fossil osteoglossiforms have been known from all the continents except Antarctica, and the Recent osteoglossiforms survive in all the southern continents. Why do Hiodontiformes seem to have been restricted to the northern hemisphere but Osteoglossiformes have a globally widespread distribution?

2) The Recent Notopteroidei (including Mormyridae and Gymnarchidae) have a southern continental distribution. However, the earliest fossil notopteroids have been found in North America (†*Ostariostoma*) and Europe (†*Thaumaturus*) according to this thesis. How can we explain the biogeographical history of the Notopteroidei when the †Ostariostomidae are included in the suborder?

3) The Australian †*Phareodus queenslandicus* is thought to be the sister species of the North American †*Phareodus encaustus*. The genus †*Phareodus* is also considered to possibly contain a European species [†*Phareodus* (†*Brychaetus*) *muellerii*]. Fossil fishes thought to resemble †*Phareodus* have also been found in South America (Gayet, 1991) and East Asia (Son, 1991, pers. com.) (see Fig. 7-11). If all these identifications are correct, how can we explain the wide distribution of †*Phareodus*?

4) Other difficult problems concern the extinction of Hiodontiformes from East Asia, the extinction of Osteoglossiformes from East Asia and Europe, and the role played by Antarctica in the evolutionary history of Osteoglossomorpha.

All these difficult problems need to be clarified in the future.

CONCLUSIONS

1. The supercohort Osteoglossomorpha is the sister-group of the clade containing Clupeomorpha and Euteleostei. This relationship is supported by three character states. a) the anterior portion of the frontal does not serve as the separation between the nasals; b) uroneurals decrease from four to zero; and c) hypurals are never more than seven.

2. The monophyly of Osteoglossomorpha can not be disproved by including several ill-defined taxa of basal teleosts. My cladistic analysis sorts out the following eight synapomorphies to confirm the monophyly of Osteoglossomorpha: a) absence of supraorbital, b) presence of primary bite of mouth between parasphenoid and basihyal, c) absence of supramaxilla, d) fusion between io4 and io5, e) development of paired tendon bones on 2nd hypobranchial or 2nd hypobranchial and basibranchial, f) number of epurals decreased to one or zero, g) 16 or fewer principal branched caudal fin rays, and h) intestine coiling to left of esophagus and stomach.

3. The so-called close relationship between †Lycopteridae and Hiodontidae is not valid because the characters used to link these two taxa are either plesiomorphic (e.g., the "temporal fenestra" and the single epural) or highly homoplastic (e.g., seven hypurals). However, the relationship between †Lycopteridae (or †Lycopteriformes) and all other osteoglossomorphs including hiodontids is still supported by four (a, b, f, and g) of the six osteoglossomorph skeletal synapomorphies listed in **2** . These synapomorphies strongly suggest that †Lycopteridae (or †Lycopteriformes) are a stem-group of the clade consisting of Hiodontiformes and Osteoglossiformes.

4. The order Hiodontiformes is used *sensu stricto* in this thesis, and does not contain †Lycopteridae. It is also considered to be independent of the Notopteroidei because no unique character state can be found to link Hiodontidae with Notopteroidei.

The monophyly of Hiodontiformes is established based on five synapomorphic features: a) dermosphenotic triradiate, b) dorsal part of hyomandibular distinctly separated or double-headed and bridged, c) dorsal arm of post-temporal more than twice as long as ventral arm, d) opercle an irregular parallelogram, and e) pelvic fin seven-rayed. Phylogenetically, Hiodontiformes are the sister clade of Osteoglossiformes because they share all the osteoglossomorph synapomorphies including the absence of a supramaxilla and the fusion of io4 with io5.

In total, five North American hiodontiform species are recognized (Table 7-2). Of these, †*Eohiodon rosei* and †*Eohiodon woodruffi* form a clade that is linked by one synapomorphy, the head of the hyomandibular articulating with the cranium having two equally-sized heads. The sister-group relationship between †*Eohiodon* and *Hiodon* is mainly supported by the sexually dimorphic anal fin and the ratio of frontal length to parietal length. The establishment of the relationship between †*Hiodon consteniorum* sp. nov. and the two extant species of *Hiodon* is based on five synapomorphies (nasal tubular and curved, anterior portion of premaxilla lower than posterior portion, development of a posterodorsal projection of opercle, presence of a mid-dorsal concavity on premaxilla, and neural spine on pu1 rudimentary).

5. Osteoglossiformes differ from Hiodontiformes in the following character states: nasal gutter-like or irregularly subrectangular in shape, uroneural single or absent, number of hypurals decreased to mainly six or five, and caudal fin consisting of 15 or fewer principal branched rays. This clade contains the emended Osteoglossoidei and Notopteroidei. Species in Osteoglossoidei are characterized by a subsemicircular or an oval opercle, the pterygoquadrate area behind and below the orbit being completely covered by infraorbitals, and the first ural centrum bearing one or two fully developed neural spines. The species in Notopteroidei have a rectangular and moderately-sized io2, an irregularly rectangular io3, an infraorbital ledge formed by io1 and io2, the infraorbital canal on io1 to io3 opening in a groove, and utriculus completely separated from the sacculus and lagena.

†*Joffrichthys* and †*Cretophareodus* are two new genera added to the fossil record of North American osteoglossiform fishes. The former is likely the sister-group of the clade consisting of †*Sinoglossus*, *Heterotis*, and *Arapaima* because it shares with these genera an oval-shaped opercle, a maxilla posteriorly ending over the dentary part of the lower jaw, a preopercle with about equally lengthened horizontal and vertical arms, and an irregularly wide and trapezoidal io2. The latter might have derived from a common ancestor with †*Phareodus* because they share at least one synapomorphy: anterior

portion of frontal at least 1.5 times as broad as the posterior portion.

The previously named North American †*Phareodus* species are most closely related to the Australian †*Phareodus queenslandicus* and the European †*Brychaetus*. These early Tertiary osteoglossines share three important synapomorphies: a) extrascapular slender and distinctly angular, b) ratio of depth to width of opercle greater than 2, and c) anterior portion of frontal at least twice as broad as posterior portion. Further investigation discriminates another two sister-group relationships. One is between †*Brychaetus muelleri* and †*Phareodus encaustus* plus †*Phareodus queenslandicus* based on the curved preopercle and the subtriangular anterior wing of the hyomandibular. The other is between †*Phareodus encaustus* and †*Phareodus queenslandicus* based on the shape of io3. These two sister-group relationships suggest that †*Brychaetus* is a junior synonym of †*Phareodus*.

6. †*Ostariostoma* is an osteoglossiform because it shares a gutter-like nasal, fewer than two uroneurals, five hypurals, and 15 or fewer principal branched caudal fin rays with all the other members of Osteoglossiformes. In the clade Osteoglossiformes, †*Ostariostoma* is linked with Notopteroidei by four character states: 1) io2 more or less rectangular and moderate in size, 2) shape of io3 irregularly rectangular, 3) presence of infraorbital ledge formed by io1 and io2, and 4) infraorbital canal on io1 to io3 open in a groove. Further study indicates that †*Ostariostoma* forms a clade with †*Thaumaturus*, defined by: 1) single uroneural, 2) strongly upturned mouth cleft, and 3) preoperculo-mandibular canal on vertical arm of preopercle open in a groove. This clade is most closely related to Mormyroidea by two homoplasies: 1) length of vertical arm of preopercle about as long as horizontal arm, and 2) basihyal tooth plate fused with basibranchial tooth plate.

7. The hypothetical earliest ancestral osteoglossomorphs were most likely more plesiomorphic than †*Lycoptera*, †*Yanbiania*, †*Chandlerichthys*, †*Koonwarria*, †*Laeliichthys*, and *Kipalachthys*; they could have well existed much earlier and had a much more widespread distribution than any of these Late Jurassic or Early Cretaceous genera. Consequently, Osteoglossomorpha might have accomplished their early development in Pangaea by the time of the Late Jurassic, before the final splitting of that supercontinent. †Lycopteriformes is likely a lineage endemic only to East Asia.

8. This study provides the following sequenced classification of Osteoglossomorpha, proposed as a framework for further discussion.

Subdivision Teleostei
  Superorder Osteoglossomorpha

- Order †Lycopteriformes
  - Family †Lycopteridae
    - Genus †*Lycoptera*
    - Genus †*Tongxinichthys*
- Order Hiodontiformes
  - Family Hiodontidae
    - Genus †*Yanbiania*
    - Genus †*Plesiolycoptera*
    - Genus †*Eohiodon*
    - Genus *Hiodon*
- Order Osteoglossiformes
  - †*Tanichthys*
  - Suborder Osteoglossoidei
    - †*Chandlerichthys*
    - †*Laeliichthys*
    - Family Osteoglossidae
      - Subfamily Heterotidinae
        - Genus †*Joffrichthys*
        - Genus †*Sinoglossus*
        - Genus *Heterotis*
        - Genus *Arapaima*
      - Subfamily Osteoglossinae
        - Genus†*Cretophareodus*
        - Genus †*Phareodus*
        - Genus †*Singida*
        - Genus *Pantodon*
        - Genus *Osteoglossum*
        - Genus *Scleropages*
  - Suborder Notopteroidei
    - Family †Ostariostomidae
      - Genus †*Ostariostoma*
      - Genus †*Thaumaturus*
    - Family Mormyridae (represented by)
      - Genus *Gnathonemus*
      - Genus *Mormyrus*

- Genus *Mormyrops*
- Family Gymnarchidae
  - Genus *Gymnarchus*
- Family Notopteridae
  - Genus *Notopterus*
  - Genus *Papyrocranus*
  - Genus *Xenomystus*

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APPENDIX 7-I

84 characters used in cladistic analysis are:

1. Epipleurals: (Epip)
   [0] = absent
   [1] = present

2. Ethmoid commissure: (Ethc)
   [0] = absent
   [1] = present

3. Gular plate: (Gp)
   [0] = absent
   [1] = present

4. Position of uroneurals (when they are present): (Pun)
   [0] = dorso-lateral to terminal caudal vertebrae
   [1] = lateral to terminal caudal vertebrae

5. Swimbladder-ear connection (directly): (S-ec)
   [0] = absent
   [1] = present

6. Length of neural spine on Pu2: (Lpu2)
   [0] = shorter than neural spine on Pu3
   [1] = as long as neural spine on Pu3

7. Uroneurals: (Un)
   [0] = more than four
   [1] = three to four
   [2] = one or two
   [3] = absent

8. Number of hypurals: (#H)
   [0] = more than seven
   [1] = seven
   [2] = six
   [3] = mainly five or fewer

9. Basipterygoid process: (Bp)
   [0] = present
   [1] = absent

10. Urodermals: (Ud)
    [0] = present
    [1] = absent

11. Upper caudal scutes: (Dcs)
    [0] = present
    [1] = absent

12. Relationship between two nasals: (Nana)
    [0] = separated by anterior portion of frontal
    [1] = separated mainly by mesethmoid
    [2] = meeting with each other

13. Pre-epiotic fossa (=temporal fenestra): (Pe-f)
    [0] = absent
    [1] = present

14. Supraorbital canal: (So.c)
    [0] = ending in parietal
    [1] = ending in frontal

15. Epural: (Ep)
    [0] = two to three
    [1] = one
    [2] = absent

16. Supramaxilla: (Smx)
    [0] = present
    [1] = absent

17. Pelvic fin rays (when present): (Vfr)
    [0] = more than seven
    [1] = seven
    [2] = six or fewer

18. Supraorbital: (So)
    [0] = present
    [1] = absent

19. Primary bite of mouth between parasphenoid and basihyal: (Pbm)
    [0] = absent
    [1] = present

20. Principal branched caudal fin rays: (Cfr)
    [0] = 17 or more
    [1] = 16
    [2] = 15 or fewer

21. Paired tendon bones on 2nd hypobranchial or 2nd hypobranchial and basibranchial: (Tbhb)
    [0] = absent
    [1] = present

22. Intestine: (Int)
    [0] = coiling to right of esophagus and stomach
    [1] = coiling to left of esophagus and stomach

23. Opercle: (Op)
    [0] = more or less irregular trapezoidal

[1] = irregular parallelogram
[2] = more or less oval or kidney-shaped
[3] = subsemicircular
[4] = fan-shaped

24. 4th and 5th infraorbitals: (Io4-5)
[0] = separate from each other
[1] = fused with each other

25. Length of frontal / length of parietal: (Fl/Pl)
[0] = >2
[1] = <2

26. Nasal: (Na)
[0] = tubular but not curved
[1] = tubular and strongly curved
[2] = gutter-like or irregularly subrectangular

27. Upper hypurals and second ural: (U2-h)
[0] = not fused
[1] = fused

28. Branches of preoperculo-mandibular canal on horizontal arm of preopercle: (Pomc)
[0] = distributed as separate openings
[1] = connected with each other to form a horizontal groove

29. Neural spine on u1: (Nu1)
[0] = absent or rudimentary
[1] = one complete
[2] = double

30. The second infraorbital: (Io2)
[0] = more or less slender and small in size
[1] = more or less rectangular and moderate in size
[2] = irregularly wide trapezoidal in shape and large in size

31. Shape of dorsal fin (when it is present): (Dsh)
[0] = triangular or falcate
[1] = rounded

32. Posterior rays of dorsal and anal fins: (Prda)
[0] = shorter than anterior ones
[1] = longer than or as long as anterior ones

33. Pterygo-quadrate area behind and below orbit: (P-qa)
[0] = not completely covered by infraorbitals
[1] = completely covered by infraorbitals

34. Palatine and ectopterygoid: (Paec)
[0] = separate from each other
[1] = fused to form palato-ectopterygoid

35. Dorsal arm of post-temporal: (Dapt)
    [0] = less than 1.5 times as long as ventral arm
    [1] = more than twice as long as ventral arm

36. Head of hyomandibular articulating with cranium: (Hmh)
    [0] = single-headed
    [1] = separate double-headed
    [2] = bridged double-headed

37. Shape of dermosphenotic: (Sdsp)
    [0] = irregular triangular
    [1] = triradiate

38. "Cheek wall" formed by enlargement of 1st to 3rd infraorbitals: (CKW)
    [0] = absent
    [1] = present

39. Scales: (Sca)
    [0] = not reticulate
    [1] = reticulate

40. Length of vertical arm of preopercle (if it is angular in shape): (Lvap)
    [0] = longer than horizontal arm
    [1] = about as long as horizontal arm

41. Anterior end of horizontal arm of preopercle: (Hap)
    [0] = extending anteriorly to beneath orbit or to level of posterior edge of orbit
    [1] = extending anteriorly behind orbit

42. Basihyal tooth plate (when it is present) and basibranchial tooth plate: (Bhbb)
    [0] = separate from each other
    [1] = fused with each other

43. Posterior edge of nasal (when it is gutter-like or irregularly subrectangular): (Pena)
    [0] = straight or slightly curved
    [1] = strongly curved and extending backward

44. First pectoral fin ray: (Pfr1)
    [0] = normal (not enlarged)
    [1] = strong (greatly enlarged) and extremely long

45. Angle of jaws: (Ja)
    [0] = anterior to middle vertical line of orbit
    [1] = between middle vertical line and posterior edge of orbit
    [2] = behind orbit

46. Frontal: (Fr)
    [0] = posteriorly broader or only slight narrower than anteriorly
    [1] = anteriorly about 1.5 times as broad as posteriorly
    [2] = anteriorly at least twice as broad as posteriorly

47. Ratio of depth to width of opercle: (Rdwo)

[0] = <2
[1] = >2

48. Shape of extrascapular (supratemporal) when it is present: (Ses)
[0] = expanded and more or less squred or irregular triangular
[1] = slender and distinctly angular or branched

49. Preopercle: (Pop)
[0] = angular with a distinct horizontal arm
[1] = curved with no distinct horizontal arm

50. Hyomandibular: (Hm)
[0] = anterior not extended
[1] = with a greatly extended subtriangular anterior wing

51. Shape of io3 (lower infraorbital behind orbit): (Sio3)
[0] = posteriorly deeper and wide-fanwised
[1] = irregular rectangular
[2] = elongate and posteriorly shallow-fanwised

52. Infraorbital ledge formed by the lateral extension of the orbital margin of io1 and io2: (IOL)
[0] = absent
[1] = present

53. Infraorbital canal on infraorbitals 1-3: (Ioc)
[0] = enclosed in a bony tuber
[1] = opening in a groove

54. Utriculus: (Utr)
[0] = connected with sacculus and lagena
[1] = completely separated from sacculus and lagena

55. Mouth cleft: (Mc)
[0] = anteriorly directed or slightly upturned
[1] = strongly upturned

56. Shape of anal fin in male and female: (Ash)
[0] = same shape in both sexes
[1] = sexually dimorphic

57. Premaxilla: (Pmx)
[0] = anterior portion raised
[1] = anterior portion not raised
[2] = anterior portion lower than posterior portion

58. Postero-dorsal projection of opercle: (Pdpo)
[0] = absent
[1] = present

59. Mid-dorsal concavity on premaxilla: (Mcpm)
[0] = absent

[1] = present

60. Belly keel: (BK)
[0] = absent
[1] = present

61. Neural spine on pu1: (Npu1)
[0] = always completely developed
[1] = rudimentary
[2] = absent

62. Number of neural spine on pu2: (#Pu2)
[0] = single
[1] = double or potential to be double

63. Posterior end of maxilla: (Pemx)
[0] = lying on angular
[1] = lying on dentary

64. Antorbital and first infraorbital: (Aio1)
[0] = separate from each other
[1] = fused with each other

65. Tooth plate of basihyal: (Bhtp)
[0] = present
[1] = absent

66. Angle formed by vertical and horizontal arms of preopercle: (Apop)
[0] = $\geq 90^\circ$
[1] = $< 90^\circ$

67. Postero-ventral margin of opercle: (Pmop)
[0] = rounded
[1] = distinctly concave

68. Orbitosphenoid: (Osh)
[0] = present
[1] = absent

69. Mandibular barbels: (MB)
[0] = absent
[1] = present

70. Supratemporal commissural sensory canal passing through parietals: (Scsc)
[0] = absent
[1] = present

71. Mandibular (dentary) canal: (Mdc)
[0] = enclosed in bony tuber
[1] = opening in a groove paralle with ventral edge of dentary

72. Subopercle: (Sop)

[0] = present
[1] = absent

73. Branches of preoperculo-mandibular canal on vertical arm of preopercle (Bpcv)
[0] = enclosed in bony tuber
[1] = opening in a groove

74. Supraneurals: (SN)
[0] = present
[1] = absent

75. Abdominal scutes: (Abs)
[0] = absent
[1] = present

76. Posterior end of anal fin: (Peaf)
[0] = separate from caudal fin
[1] = connected with caudal fin

77. Fusion of last three caudal vertebrae (pu1 + u1 + u2): (Fcv)
[0] = absent
[1] = present

78. Urostyle (formed by fusion of nspu1 + u1 + u2): (Ust)
[0] = absent
[1] = present

79. Recessus lateralis: (Recl)
[0] = absent
[1] = present

80. 2nd hypural: (H2)
[0] = articulating but not fused with u1
[1] = always fused with u1

81. A tend toward exclusion of maxillae from gap by premaxillae: (Temg)
[0] = absent
[1] = present

82. Ctenoid scales: (Ctes)
[0] = absent
[1] = present or potential to be developed

83. Stegural (formed by fusion of uroneurals): (St)
[0] = absent
[1] = present

84. Adipose fin: (Adf)
[0] = absent
[1] = present